













# STUDIES OF INHERITANCE IN RABBITS

BY  
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IN COLLABORATION WITH  
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## CONTENTS.

	Page
PREFACE . . . . .	5
PART I. — EAR-SIZE . . . . .	9-35
Introduction . . . . .	9
Characteristics of lop-eared rabbits; sterility and its inheritance . . . . .	9
Growth-rate of lop-eared and of short-eared rabbits in size and in ear-length . . . . .	12
Matings of short-eared rabbits <i>inter se</i> . . . . .	14
Matings of lop-eared rabbits <i>inter se</i> . . . . .	16
Cross 1. — Lop-eared female × short-eared male . . . . .	18
Cross 2. — Short-eared female × lop-eared male . . . . .	18
Cross 3. — Belgian hare female × lop-eared male . . . . .	20
Cross 4. — Lop-eared female × half-blood lop male . . . . .	21
Cross 5. — Half-blood lop female × lop male 179 . . . . .	22
Cross 6. — Half-blood lops mated <i>inter se</i> . . . . .	23
Other matings of half-blood lops and additional Cross 6 matings . . . . .	26
Matings of three-quarter-blood lops . . . . .	31
Cross 7. — Quarter-blood lop female × short-eared male . . . . .	33
Cross 8. — Quarter-blood lop × three-quarter-blood lop . . . . .	34
Limitations of the data studied . . . . .	34
Conclusions . . . . .	35
PART II. — WEIGHT . . . . .	37-40
PART III. — SKELETAL DIMENSIONS . . . . .	41-44
PART IV. — COLOR . . . . .	45-68
Color variation in relation to color factors . . . . .	45
Development of the factor hypothesis . . . . .	46
The general color factor, C . . . . .	46
The specific pigment factors, B, Br, and Y . . . . .	46
The intensity factor, I or D . . . . .	46
The factor for a pigment pattern of the individual hair, A . . . . .	47
The factor for uniformity of pigmentation, U, or spotting with white, S . . . . .	47
The factor for extended distribution of black or brown, E, alternative with R (restricted distribution) . . . . .	47
Interrelations of factors E and U . . . . .	48
Interrelations of factors B, Br, and Y . . . . .	49
Gametic structure and variation . . . . .	49
Gametic and zygotic formulæ . . . . .	50
Color varieties of the rabbit . . . . .	51
Gray type . . . . .	52
Black type . . . . .	52
Yellow type . . . . .	53
White type . . . . .	53
Zygotic variation within each color variety . . . . .	54
Gray . . . . .	54
Blue-gray . . . . .	60
Black . . . . .	61
Blue . . . . .	62
Yellow . . . . .	63
Sooty . . . . .	64
White . . . . .	65
The material basis of heredity factors . . . . .	68
BIBLIOGRAPHY . . . . .	69
DESCRIPTION OF PLATES . . . . .	70



## PREFACE.

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In this paper are recorded observations upon inheritance in rabbits which were made in the Harvard Zoölogical Laboratory with the aid of a grant from the Carnegie Institution of Washington. The authors desire to express their appreciation of that aid, without which these observations could not have been made.

The experiments described were planned by the senior author, and this report also was written by him. Dr. H. E. Walter has made the majority of the extremely laborious observations and computations concerning the inheritance of ear-length and of body-weight. Dr. R. C. Mullenix prepared and measured the rabbit skeletons as a foundation for Part III of this paper; while both Dr. Walter and Mr. Cobb rendered valuable assistance in connection with the study which has been made of color inheritance. The senior author alone is responsible for the analytical treatment of the observations.



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## PART I.—EAR-SIZE.

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### INTRODUCTION.

The inheritance of ear-size in rabbits has been characterized as blending, in certain preliminary publications, (Castle, :05, :05*a*).<sup>1</sup> The experimental evidence for such a characterization is described in the following pages. It consists of results obtained by experimental cross-breeding of lop-eared rabbits with ordinary short-eared ones. A detailed account of this evidence is of little interest to the general reader, who therefore may advantageously omit pages 14-34. For consultation on the part of the critical student of heredity, it has been thought essential to present this evidence in some detail, even though it is intrinsically uninteresting.

### CHARACTERISTICS OF LOP-EARED RABBITS; STERILITY AND ITS INHERITANCE.

Lop-eared rabbits are distinguished from ordinary ones chiefly by the enormous size of their ears, which are so large as to hang down, touching the ground on either side of the head. (See plate 1, fig. 2, and plate 2, fig. 8.) This breed of rabbit is characterized also by a long tail and unusual size, being one of the largest breeds known. The characters of large size and long tail, however, have probably not been sought for their own sake, but have been incidentally obtained in the production of the breed as a result of selection for ears of large size; for among lop-eared rabbits, as a rule, those of the largest size have longest ears.

In the winter of 1904 a pair of lop-eared rabbits was obtained from a fancier and used in various breeding experiments. Matings of the two together were for the most part fruitless, only one litter of 2 young being successfully reared. These were similar to the parent rabbits in size and ear-character. Of the two, one was a male, which was used extensively in breeding experiments, including one successful mating with his mother, from which came a good-sized litter. But only two out of this litter attained the age of 20 weeks and they ultimately succumbed to disease under conditions not unfavorable to other rabbits. The second of the two young reared by the original lop-eared pair was a female. Only twice did this rabbit bear young by any sort of mating. In one case she failed to rear any of the young. In the other case she reared, when mated to her own

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<sup>1</sup> For complete titles see Bibliography, p. 69.

brother, 2 young out of a litter of 3. Both were males. The larger one, although apparently healthy, failed to breed; the smaller one was not tested. Accordingly, out of 5 pure-bred lop-eared rabbits with which we have experimented, 2 (a male and a female) were infertile — one of the two largely so, and the other completely. Infertility has also been encountered among a few of the female descendants of this lop-eared stock produced by cross-breeding, but in no other stock of rabbits with which we have experimented. Sterile individuals have not been observed among half-blood lops of generation  $F_1$ , but a few have occurred in later generations. In the majority of cases, however, the sterile individuals have been three-quarter-blood lops.

From these facts we conclude that a tendency to sterility is inherent in the lop-eared stock used, and is transmitted, not to the immediate offspring ( $F_1$ ) if they are cross-breeds, but to the next generation, when it is produced by a back-cross between  $F_2$  and the pure lop-eared stock; less frequently sterility reappears in  $F_2$ , produced by breeding the half-blood lops *inter se*. We should expect the infertility to occur only half as frequently in this latter sort of mating as in the former, where it has been oftenest observed. On the whole, it seems probable that a tendency to sterility is inherited in rabbits, as in *Drosophila* (see Castle *et al.*, :06), after the manner of a Mendelian recessive character, *i. e.*, skipping a generation in crosses.

Why lop-eared rabbits more than other breeds should show a tendency to sterility is not known; but as they are extensively inbred, it seems highly probable that inbreeding is largely responsible for this sterility. The lop-eared character is one which, from the manner of its inheritance, we may be sure, has been built up slowly as the result of selection. In this process inbreeding must have been continuously practised, for since every out-cross would result in loss of half the ground gained by selection, it would be practised only when absolutely necessary.

At birth rabbits have ears quite undeveloped, and the ears do not attain their full growth until an age of 5 to 8 months have been reached. Ear-growth is well advanced, however, at 20 weeks, after which time it becomes very slow. Accordingly 20 weeks has been found a convenient age at which to institute comparisons as to ear-character between different lots of rabbits. Frequently, however, it is impossible to rear an entire litter of rabbits to the age of 20 weeks, in which case an earlier determination of ear-character becomes desirable. For this reason, after some experimentation, we adopted the plan of making weekly measurements of the ear dimensions at ages from 2 to 20 weeks inclusive. This process, while laborious, fully eliminates errors due to observation, as well as those due to temporary growth conditions.

The weekly observations upon each rabbit included taking its weight, the maximum length and maximum width of its right ear, and finally the



spread of the ears, *i. e.*, the distance from ear-tip to ear-tip when the ears are extended in a horizontal position and stretched slightly. Since the measurements in nearly all cases were made by the same observer (Walter), the personal equation is a fairly constant factor and may be disregarded

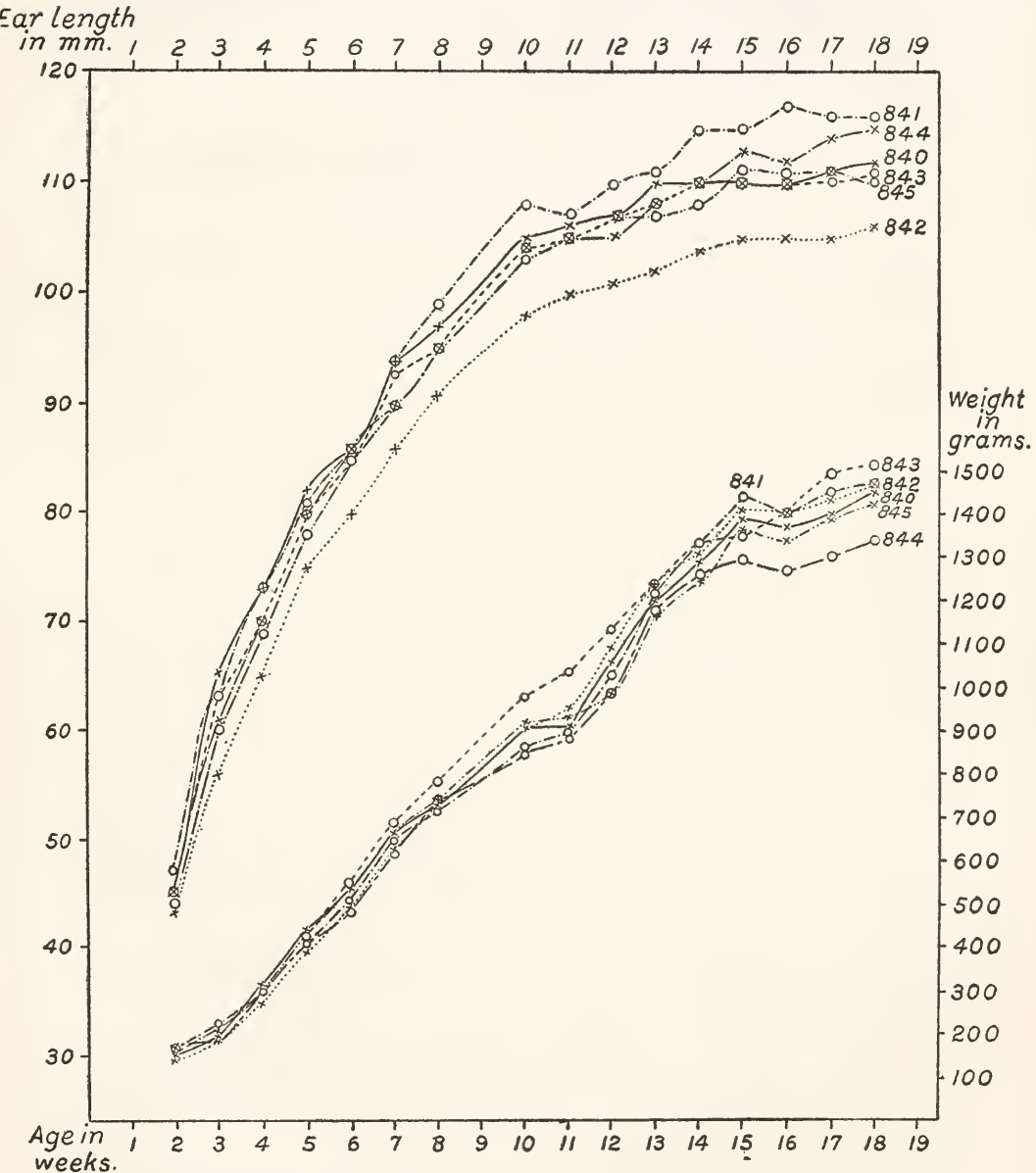


FIG. 1. Chart showing growth in ear-length, and body-weight of a litter of six short-eared rabbits between the ages of two and eighteen weeks. See table 1.

in comparing one set of observations with another. Records of this sort, more or less complete, were made for 70 different litters of rabbits, containing 341 individuals.

An inspection of figs. 1 to 3 shows that the growth-curve for ear-length<sup>1</sup> from 2 weeks after birth is of the same general form in the case of both long-eared and short-eared rabbits. It is a curve convex above, indicating a steadily diminishing daily increment in ear-length.

#### GROWTH-RATE OF LOP-EARED AND OF SHORT-EARED RABBITS IN SIZE AND IN EAR-LENGTH.

The theoretical growth-curve of an organism in weight (Houssay, :07; Robertson, :08) is at first concave upward, but later becomes convex. When the curve is concave upward the daily growth increment is increasing. But when the growth-curve becomes convex upward, it is evident that the growth increment is decreasing. Therefore the period of greatest daily growth occurs when the growth-curve is changing from a concave to a convex one. In rabbits this occurs at an age of from 6 to 8 weeks after birth (see figs. 1 to 3). According to Robertson (:08) the period of maximum growth corresponds with the middle point of a growth-cycle which in character resembles an autocatalytic monomolecular chemical reaction. In the rabbit this growth-cycle probably has its beginning at some time prior to birth and ends before puberty is attained.

It is possible that this same form of curve would be observed in respect to ear-length also, if the measurements began at a period sufficiently early. Growth of the ears is completed before increase in body-weight ceases, and it is possible that the growth-curve for ear-length has already changed from a concave to a convex form at the age of 2 weeks, when our measurements begin. But it is, on the other hand, possible that the growth-curve for ear-length would not show a convex form upward even if completed for the period prior to 2 weeks of age; for ear-length is a linear dimension, whereas body-weight depends on volume, *i. e.*, size in three dimensions, and a doubling of any linear dimension should be attended by an eight-fold increase of volume.

A comparison of fig. 1 with fig. 2 shows a considerable difference between ordinary short-eared (fig. 1) and lop-eared (fig. 2) rabbits as regards size, at corresponding ages; the difference is even more striking in regard to ear-length. Crosses between the two varieties produce rabbits intermediate in character as regards both weight and ear-length. But before considering further the character of the cross-breeds, it will be well to inquire how each variety breeds by itself.

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<sup>1</sup> The measurements for ear-width and "spread" are closely correlated with those for ear-length. For the sake of simplicity we shall deal with the statistics for ear-length only.

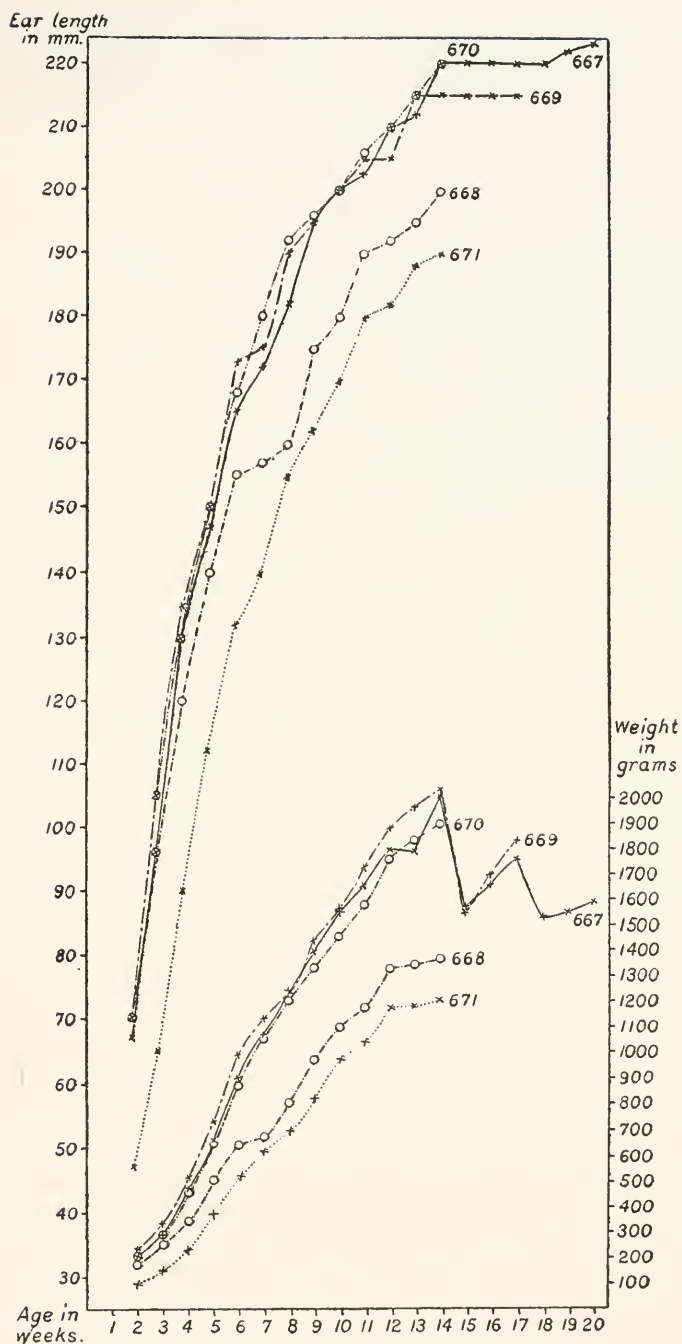


FIG. 2. Growth-curves for a litter of five lop-eared rabbits.  
See table 2 and compare fig. 1.

MATINGS OF SHORT-EARED RABBITS *INTER SE*.

Several matings of short-eared rabbits *inter se* are recorded in table 1. They show great uniformity of result. The young differ little in ear-length from their parents, which in no case differed from each other by more than 5 mm.

TABLE 1.

MATING 1.				MATING 2.			
	Ear-length.	Weight.	Age.		Ear-length.	Weight.	Age.
	<i>mm.</i>	<i>gms.</i>			<i>mm.</i>	<i>gms.</i>	
Parents:				Parents:			
♀ 255 .....	115	2,650	Adult. <sup>1</sup>	♀ 498 .....	110	1,980	27 weeks.
♂ 497 .....	110	2,045	7 mos.	♂ 497 .....	110	1,915	Do.
Mid-parental	112.5	2,347		Mid-parental	110	2,045	7 mos.
Offspring:				Offspring:		1,947	27 weeks.
Litter 1 —				Litter 1 —			
♀ 768 .....	107	1,445	20 weeks.	♀ 782 .....	110	1,365	20 weeks.
♀ 769 .....	111	1,480	Do.	♀ 783 .....	106	1,575	Do.
♀ 770 .....	115	1,780	Do.	♀ 784 .....	107	1,375	Do.
♂ 771 .....	113	1,740	Do.	♂ 785 .....	110	1,695	Do.
♀ 772 .....	106	1,550	Do.	Litter 2 (see			
♂ 773 .....	111	1,650	Do.	fig. 1) —			
Litter 2 —				♀ 840 .....	112	1,450	18 weeks.
♂ 881 .....	110	1,380	14 weeks.	♀ 841 .....	116	1,460	Do.
♀ 882 .....	110	1,380	16 weeks.	♀ 842 .....	106	1,460	Do.
♂ 883 .....	114	1,500	14 weeks.	♂ 843 .....	111	1,510	Do.
♂ 884 .....	115	1,560	Do.	♀ 844 .....	115	1,340	Do.
				♀ 845 .....	110	1,420	Do.
MATING 3.				MATING 4.			
Parents:				Parents:			
♀ 268 .....	105	2,280	Adult.	♀ 268 .....	105	2,280	Adult.
♂ 497 .....	110	2,045	7 mos.	♂ 56 .....	102	2,500	Do.
Mid-parental	107.5	2,162		Mid-parental	103.5	2,390	Do.
Offspring:				Offspring:			
♀ 859 .....	110	1,445	15 weeks.	♂ 774 .....	108	1,715	20 weeks.
♂ 861 .....	112	1,340	Do.				
♂ 862 .....	110	1,420	Do.				
♂ 863 .....	110	1,295	Do.				

<sup>1</sup> By adult is meant 1 year or more old.

In mating 1, the extreme deviations from the mid-parental<sup>1</sup> ear-length are -6.5 mm. and +2.5 mm., the average deviation being only 2.5 mm. The total range of variation is 9 mm. In mating 2, between brother and sister, the extreme deviations are -4 mm. and +6 mm., giving a total range of variation of 10 mm. The average deviation from the parental ear-length (110 mm.) is, as in mating 1, 2.5 mm.

<sup>1</sup> By mid-parental, as we shall use the term in this paper, is meant a magnitude exactly halfway between the magnitudes of the respective parents. It is the mean of the parental magnitudes.

The growth-curves for litter 2, which were produced by this mating, are shown in figure 1. In mating 3, the deviations are all plus in character, but are small in amount, namely, 2.5, 4.5, 2.5, and 2.5 mm.

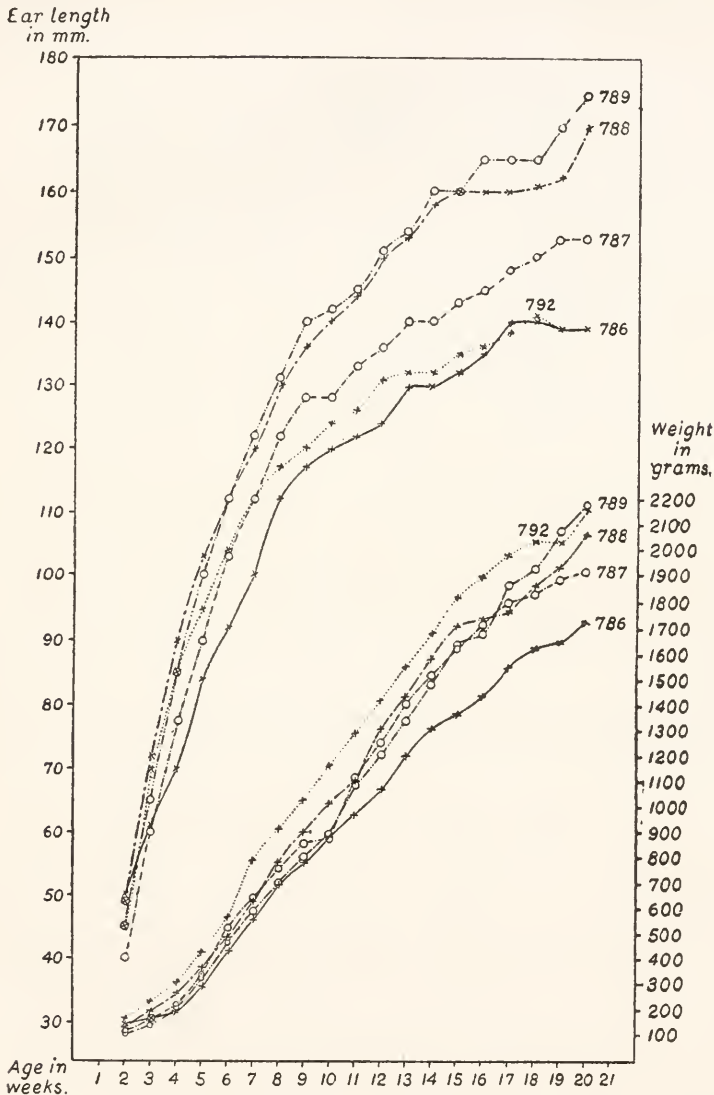


FIG. 3. Growth-curves for a litter of five second-generation ( $F_2$ ) half-lop rabbits.  
See table 9 and compare figs. 1 and 2.

From mating 4, by the same female that was concerned in mating 3, a single young one was reared, which showed a plus deviation of 4.5 mm.

Another mating which falls in this category was made between the Belgian hare (♀ 431) and the short-eared ♂ 56 (see table 1A). It shows a complete blending in the offspring of the parental ear-lengths, with a very small range of variation, viz, 6 mm.

TABLE 1A.

	Ear-length.	Weight.	Age.
	<i>mm.</i>	<i>gms.</i>	
Parents:			
♀ 431.....	118	3,400	Adult.
♂ 56.....	102	2,500	Do.
Mid-parental....	110	2,950	Do.
Offspring:			
♀ 232.....	{ 102	.....	21 weeks.
	{ 105	2,700	Adult.
♀ 233.....	111	.....	21 weeks.
♂ 234.....	108	.....	Do.
♂ 235.....	{ 108	.....	Do.
	{ 110	2,945	Adult.
♀ 236.....	108	.....	21 weeks.

The mid-parental ear-length was exceeded by 1 of the young at 21 weeks of age; 3 others came within 2 mm. of the mid-parental ear-length at 21 weeks of age, and 1 of these equaled it when adult. If the other 2 did as well they too must have attained the expected ear-length. Only 1 individual (♀ 232), then, fails to attain the mid-parental ear-length. This result is almost identical in general character with that shown by table 1.

We may conclude that short-eared rabbits breed true within a range of fluctuating variability not exceeding 10 mm.

#### MATINGS OF LOP-EARED RABBITS INTER SE.

Our original stock of lop-eared rabbits consisted of a single pair. Both of them gave vigorous young in matings with short-eared rabbits, but not with each other. Consanguinity may have been the reason for this latter fact. They were obtained from the same source, and doubtless were nearly related, as well as inbred. Nevertheless we did obtain from them two good-sized and healthy young, ♂ 179 and ♀ 180. The former appears in many of the crosses to be described, but the latter proved a very poor mother, producing only occasional litters of young, none of which attained maturity. Table 2 shows the only results obtained from mating lop-eared individuals *inter se*.

Mating 1 produced 2 young, one (♂ 179) very similar to the father, the other (♀ 180) very similar to the mother, but not quite so large and with ears 5 mm. shorter. The deviations from the mid-parental ear-length are -7.5 and -2.5 mm., respectively.



Mating 2 (between brother and sister) produced 2 young, which reached the age of 20 weeks. Though they were not large, their ears attained a good length, the deviations from the mid-parental ear-length being -5 mm. and -2 mm.

TABLE 2.

MATING 1.				MATING 3.			
	Ear-length.	Weight.	Age.		Ear-length.	Weight.	Age.
Parents:	<i>mm.</i>	<i>gms.</i>		Parents:	<i>mm.</i>	<i>gms.</i>	
Old ♀ lop (pl. 1, fig. 2) ..	225	4,600	Adult.	Old ♀ lop (pl. 1, fig. 2) ..	225	4,600	Adult.
Old ♂ lop ..	210	3,450 <sup>1</sup>	Do.	♂ 179 (pl. 2, fig. 8) .....	210	3,410	Do.
Mid-parental	217.5	4,025	Do.	Mid-parental	215.7	4,005	Do.
Offspring:				Offspring (see fig. 2):			
♂ 179 (pl. 2, fig. 8) .....	210	3,410	Adult.	♂ 667 .....	220	2,010	14 weeks.
♀ 180 .....	220	3,765	Do.	♂ 223 .....	223	1,590 <sup>2</sup>	20 weeks.
MATING 2.				♀ 668 .....	200	1,370	14 weeks.
Parents:				♀ 669 .....	215	2,030	Do.
♀ 180 .....	210	3,410	Adult.	♂ 670 .....	220	1,900	Do.
♂ 179 .....	220	3,765	Do.	♂ 671 .....	190	1,205	Do.
Mid-parental	215	3,587	Do.				
Offspring:							
♂ 616 .....	210	1,680	20 weeks.				
♂ 618 .....	213	1,820	Do.				

<sup>1</sup> Estimated.<sup>2</sup> Sick.

Mating 3 (between mother and son) produced a litter of 5 young, which grew in a satisfactory manner until 14 weeks old (see fig. 2). Then, as a result of disease, 4 of them died, and the fifth became greatly reduced in flesh, so that at 20 weeks of age he weighed 400 grams less than at 14 weeks of age. Nevertheless his ears continued to grow slowly. At 14 weeks they measured 220 mm.; at 20 weeks, 223 mm.

The rabbit 671 was from the beginning much the smallest one in the litter; we named him the "runt" and had hopes of securing from him a race of small-sized but lop-eared rabbits. These hopes were ended by the unfortunate illness which attacked the entire litter. The small size of this rabbit accounts for the shortness of his ears (190 mm. at 14 weeks of age). Leaving him out of consideration, the range of variation in ear-length is 20 mm.; with him, it is 30 mm., at 14 weeks of age.

Two of the young produced by mating 3 had already at 14 weeks of age exceeded the mid-parental ear-length, a third had almost reached it, while the 2 others fell below it. This is a fluctuating variation around the mid-parental ear-length, and indicates that the long-eared character tends to breed true, within a range of variation of 20 (or possibly 30) mm., the minus variations, however, probably being greater than the plus ones.

CROSS 1. — LOP-EARED FEMALE  $\times$  SHORT-EARED MALE.

The largest and longest-eared rabbit with which we have experimented was a female obtained by purchase and of unknown ancestry. (See plate 1, fig. 2.) Her ear-length was 225 mm. and her adult weight 4,600 grams. She was mated with a small-eared angora rabbit ( $\sigma$  45, plate 1, fig. 3), whose ear-length was 105 mm. and adult weight 3,000 grams. A litter of 8 young was obtained from this pair. All were reared to an age of 2 months, when 6 were discarded. The remaining 2 were reared to maturity. One of them ( $\sigma$  248) is shown in plate 1, fig. 1. The 6 discarded rabbits had ears shorter than those of the rabbits which were kept. Their ear-lengths are given in table 3 as estimated from the known relation of their ear-lengths at 2 months of age to the ear-lengths of rabbits 247 and 248, the animals kept until adult. Table 3 shows that the young obtained from this cross are, as regards ear-length, intermediate between the parents, but stand nearer the short-eared than the long-eared parent. As regards weight,  $\sigma$  247 is smaller and  $\sigma$  248 larger than the mid-parental condition; the remaining 6 would probably not have exceeded  $\sigma$  247 in weight had they been reared to maturity. Accordingly as regards both size and ear-length in this cross the resemblance is greater toward the smaller and shorter-eared parent (father).

TABLE 3. — Cross 1.

	Ear-length.	Weight.	Age.
	<i>mm.</i>	<i>gms.</i>	
Parents:			
♀ lop .....	225	4,600	Adult.
♂ 45 .....	105	3,000	Do.
Mid-parental. . .	165	3,800	Do.
Offspring:			
♀ 247 .....	152	3,290	Adult.
♂ 248 .....	153	3,930	Do.
♂ 249 .....	145 <sup>1</sup>		
♂ 250 .....	147 <sup>1</sup>		
♂ 251 .....	138 <sup>1</sup>		
♂ 252 .....	149 <sup>1</sup>		
♂ 253 .....	145 <sup>1</sup>		
♂ 254 .....	142 <sup>1</sup>		

<sup>1</sup> Estimated.CROSS 2. — SHORT-EARED FEMALE  $\times$  LOP-EARED MALE.

This cross, the reciprocal to the foregoing, was made repeatedly. The lop-eared male used ( $\sigma$  179, plate 2, fig. 8) was a son of the lop-eared female employed in cross 1. He was, however, smaller than his mother, and had shorter ears. The results of 4 different matings are shown in table 4. In mating 1 there were only 2 surviving young, which therefore were probably the largest and strongest individuals in the litter and received more than the average amount of nourishment. One of them



surpassed at 18 weeks of age the mid-parental ear-length, while the other one almost equaled it. Their weights at 18 weeks of age indicated that the mid-parental weight would be attained at maturity.

TABLE 4. — *Cross 2.*

MATING 1.				MATING 3.			
	Ear-length.	Weight.	Age.		Ear-length.	Weight.	Age.
Parents:	<i>mm.</i>	<i>gms.</i>		Parents:	<i>mm.</i>	<i>gms.</i>	
♀ 268 .....	105	2,280	Adult.	♀ 105 .....	100	.....	9 mos.
♂ 179 (lop) ..	210	3,410	Do.	♂ 179 (lop) ..	210	3,410	Adult.
Mid-parental	157.5	2,845	Do.	Mid-parental	155	.....	
Offspring:				Offspring:			
♂ 571 .....	155	2,310	18 weeks.	♀ 626 .....	150	1,380	20 weeks.
♀ 572 .....	160	2,110	Do.	♂ 627 .....	150	1,470	Do.
				♀ 629 .....	150	1,485	Do.
				♀ 630 .....	145	1,430	Do.
				♀ 632 .....	148	1,370	Do.
				♂ 634 .....	150	1,325	Do.
MATING 2.				MATING 4.			
Parents:				Parents:			
♀ 269 (pl. 2, fig. 5) ....	92	1,935	Adult.	♀ 108 .....	110	2,520	Adult.
♂ 179 (lop) ..	210	3,410	Do.	♂ 179 .....	210	3,410	Do.
Mid-parental	151	2,672	Do.	Mid-parental	160	2,965	Do.
Offspring:				Offspring:			
Litter 1 —				♂ 607 .....	158	2,050	20 weeks.
♀ 574 .....	140	1,950	18 weeks.	♂ 608 .....	155	1,810	18 weeks.
♀ 575 .....	143	1,940	Do.	♂ 609 .....	158	2,080	Do.
Litter 2 (pl. 2, fig. 6) —							
♂ 640 .....	150	1,980	20 weeks.				
♀ 641 .....	150	1,850	Do.				
♀ 642 .....	152	1,930	Do.				
♀ 643 .....	144	1,670	19 weeks. (less at 20)				

Under the head of mating 2 are given the results of 2 different litters, litter 1 consisting of 2 rabbits, litter 2 of 4. The weight of the mother was surpassed by that of the offspring in 4 out of 6 cases, at the early age of 18 to 20 weeks. Three of the 6 young had ear-lengths very similar to the mid-parental ear-length; the remaining 3 had ears somewhat shorter at 18 or 19 weeks old, and probably would not have attained at maturity an ear-length equal to the mid-parental. Litter 2 is shown in plate 2, fig. 6; the parents in figs. 5 and 8 of the same plate.

The 6 young produced by mating 3 were under-sized at 20 weeks of age, which perhaps accounts for the fact that no one of them attained the mid-parental ear-length, but all fell from 5 to 10 mm. short of it.

In mating 4, 2 of the 3 young came within 2 mm. of attaining the mid-parental ear-length; the third came within 5 mm. of it.

On the whole, the result of cross 2 is a fairly close approximation to the mid-parental ear-length. In no case does the deviation from the mid-parental value exceed 11 mm.; the average deviation from it is only 4.8 mm. But the differences between the respective parents ranged from 100 to 118 mm., and the least deviation of one of the offspring from either parent was 45 mm. or more than four times the greatest deviation from the mid-parental value. When deviation from the mid-parental value did occur, it was oftener under than over the mid-parental value.

Accordingly, the results observed as regards ear-length may accurately be described as a blend. As regards body-size, the data are insufficient, since adult weights of the offspring were in no case obtained, but the observed weights of the offspring in matings 1 and 2 indicate that a blend might be expected, an intermediate condition having already been obtained at 20 weeks of age.

CROSS 3. — BELGIAN HARE FEMALE  $\times$  LOP-EARED MALE.

The "Belgian hare" (plate 3, fig. 9) used in this cross was larger and had somewhat longer ears than the short-eared rabbits used in crosses 1 and 2. The lop-eared male was father of the one used in cross 2, but had about the same ear-length and body-size. A litter of 6 young was obtained, five of which were reared to an age of 21 weeks or more. In size the offspring exceeded either parent, approximating that of the female lop used in cross 1. Four of the 5 young also exceeded the mid-parental ear-length by from 2 to 6 mm., but the fifth fell short of it by 8 mm. This same individual ( $\sigma$  177) showed the least deviation from either parental ear-length, viz, 38 mm., or four and a half times the greatest deviation from the mid-parental ear-length.

TABLE 5. — *Cross 3.*

	Ear-length.	Weight.	Age.
	<i>mm.</i>	<i>gms.</i>	
Parents:			
♀ 431 (Belgian hare) ..	118	3,400	Adult.
Old ♂ lop .....	210	3,450 (?)	Do.
Mid-parental .....	164	3,425 (?)	Do.
Offspring:			
♂ 174 .....	170	.....	21 weeks.
♀ 175 .....	170	4,305	Adult.
♂ 176 .....	166	4,130	Do.
♂ 177 .....	156	.....	21 weeks.
♀ 178 .....	170	4,070	Adult.

Accordingly, in cross 3, as in cross 2, the ear-length of the offspring is approximately a blend of the ear-lengths of the respective parents. The size of the offspring, however, is greater than that of either parent, though it does not exceed the size of lop-eared individuals other than the father.

CROSS 4. — LOP-EARED FEMALE  $\times$  HALF-BLOOD LOP MALE.

This cross is a sequel to crosses 1 and 3, a male rabbit produced by cross 3 being mated with the female lop used in cross 1. This cross produced three-quarter-blood lops, the ear-lengths of which are indicated in table 6.

TABLE 6. — *Cross 4.*

	Ear-length.	Weight.	Age.
	<i>mm.</i>	<i>gms.</i>	
Parents:			
Old ♀ lop .....	225	4,600	Adult.
♂ 176 .....	166	4,130	Do.
Mid-parental .....	195.5	4,365	Do.
Offspring:			
Litter 1 —			
♀ 504 .....	186	3,430	1 year.
♂ 505 .....	206	3,770	42 weeks.
♂ 506 .....	192	3,150	30 weeks.
♀ 508 .....	180	1,690	18 weeks.
♀ 509 .....	{ 185	.....	16 weeks.
	{ 210	3,910	1 year.
Litter 2 —			
♂ 319 .....	{ 190 <sup>1</sup>	3,465	25 weeks.
	{ 200	3,955	1 year.
♀ 320 .....	182	.....	16 weeks.
♀ 321 .....	183	.....	18 weeks.
♀ 322 (pl. 3, fig. 11) ..	195	4,450	1 year.

<sup>1</sup> 23 weeks.

The range of variation in this mating is similar to that observed in a mating of this same female with a lop-eared male (see table 2), viz, a variation of between 20 and 30 mm. It is difficult to estimate it more precisely, because the measurements recorded were made at such different ages. Two of the offspring approximate the mid-parental conditions both of ear-length and of weight, these two being ♂ 319 and ♀ 322. The same is measurably true of a third individual, ♂ 506. But ♀ 504 and ♀ 508 fall considerably short of the mid-parental ear-length and the mid-parental weight; while ♂ 505 and ♀ 509 considerably exceed the mid-parental ear-length, and approximate the mid-parental size. The greatest deviation from the mid-parental ear-length is a minus one of 15 mm. (recorded at the age of 18 weeks), but a plus deviation of nearly the same amount (14.5 mm.) is also observed, though not until the age of a year had been attained. The average deviation from mid-parental ear-length is 9 mm. The lowest measurement, 180 mm., stands almost exactly midway between the ear-length of the father (166 mm.) and the mid-parental ear-length 195.5 mm.; while the largest measurement (210 mm.) stands midway between the condition of the mother (225 mm.) and the mid-parental ear-length.

The result observed in this cross may be described as blending inheritance, with fluctuation about the mid-parental ear-length, in about the same degree as in the case of lop-eared rabbits purely bred.

Two of the offspring produced by cross 4 were mated with each other, viz, ♀ 504 and ♂ 506. They produced a litter of 3 young, the character of which is shown in table 7.

TABLE 7.

	Ear-length.	Weight.	Age.
	<i>mm.</i>	<i>gms.</i>	
Parents:			
♀ 504.....	186	3,430	1 year.
♂ 506.....	192	3,150	30 weeks.
Mid-parental....	189	3,290	Do.
Offspring:			
♂ 740.....	191	2,255	20 weeks.
♂ 741.....	201	2,255	Do.
♀ 742.....	185	1,900	19 weeks.

The deviations from the mid-parental ear-length are +2, -12, and -4 mm. respectively, which lie within the limits of variation observed among lop-eared rabbits purely bred.

The range of variation is chiefly upward (plus), doubtless because of the small number in the litter, which would make the food supply of the individual better than usual.

#### CROSS 5. — HALF-BLOOD LOP FEMALE × LOP MALE 179.

Female 167 was produced by a cross similar to cross 2, in which the mother was a short-eared Himalayan rabbit (♀ 23), and the father the male lop used in cross 3. She was mated with lop ♂ 179 and produced 3 litters of young, as indicated in table 8.

The range of variation in ear-length in these 3 litters of rabbits is wide, extending from 165 mm. in a rabbit 7 months old (having full-grown ears) to 194 mm. in one only 18 weeks old, or to 200 mm. in one 30 weeks old, a total range of 35 mm. The largest minus deviation from the mid-parental ear-length is 5 mm.; the largest plus deviation, 30 mm.; the least deviation from the short-eared parent is 35 mm., but from the long-eared parent only 10 mm. Hence in this cross the long-eared parent is approximated more closely than the short-eared one. This, however, is not of necessity evidence of Mendelian recessiveness of the character long-ear in ♀ 167. Another and, we believe, better way of viewing the matter is this: ♀ 167 transmitted a greater ear-length than she had herself attained. It is known that conditions which influence general growth, during the first 20 weeks, influence also ear-length. But at 20 weeks of age ear-growth is practically complete, although growth in other respects continues some time longer. It is possible, therefore, for an animal to be stunted in ear-

size and yet to attain a normal or nearly normal general size. It is not to be expected, however, that such an animal will transmit to young reared under normal conditions the diminished ear-size which it shows, but rather the ear-size which it would have attained had it been reared under normal conditions.

TABLE 8. — *Cross 5.*

	Ear-length.	Weight.	Age.
	<i>mm.</i>	<i>gms.</i>	
Parents:			
♀ 167.....	130	2,550	Adult.
♂ 179 (lop) .....	210	3,410	Do.
Mid-parental....	170	2,980	Do.
Offspring:			
Litter 1 —			
♂ 437.....	{ 184	2,550	20 weeks.
	{ 200	3,140	30 weeks.
♀ 438.....	{ 177	2,510	20 weeks.
	{ 185	3,110	30 weeks.
Litter 2 —			
♂ 566.....	194	1,945	18 weeks.
♂ 568.....	181	1,915	Do.
♂ 569.....	170	1,865	Do.
♀ 570.....	182	....	Do.
Litter 3 —			
♀ 644.....	{ 164	1,655	20 weeks.
	{ 165	2,430	7 months.
♂ 645.....	170	1,460	20 weeks.
♀ 646.....	175	1,430	Do.
♀ 647.....	171	2,030	Do.
♀ 648.....	180	1,930	Do.
♂ 649.....	178	2,080	Do.

CROSS 6. — HALF-BLOOD LOPS MATED *INTER SE*.

The same female half-blood lop already mentioned (♀ 167, cross 8), was mated with a male produced by cross 1 (♂ 248). Their young constitute an  $F_2$  generation of half-blood lops.

In this litter the deviations from the mid-parental ear-length are all, with one exception, positive (upward). This result accords with that observed among the young of this same mother (♀ 167), in connection with cross 5. She evidently transmitted a greater ear-length than she manifested.

The range of variation, 35 mm., while high, does not exceed that found among lop-eared rabbits mated *inter se*, as is clear from a comparison of fig. 2 with fig. 3, the former showing growth-curves for lop-eared rabbits, the latter for the litter of  $F_2$  half-blood rabbits under consideration. The range of variation in this cross also agrees exactly with that observed in cross 5, in which the same mother was mated with a full-blood lop. We get, therefore, from this case no evidence of Mendelian splitting as regards the character ear-length.

TABLE 9.

	Ear-length.	Weight.	Age.
	<i>mm.</i>	<i>gms.</i>	
Parents:			
♀ 167.....	130	2,550	Adult.
♂ 248.....	153	3,930	Do.
Mid-parental....	141.5	3,240	Do.
Offspring:			
♂ 786.....	140	1,730	20 weeks.
♂ 787.....	153	1,915	Do.
♂ 788.....	170	2,060	Do.
♀ 789.....	175	2,170	Do.
♂ 792.....	140	2,155	Do.

Two of the young produced by cross 5 were mated with each other, viz, ♂ 437 with ♀ 438. Their young (table 10) vary closely about the mid-parental ear-length.

TABLE 10.

	Ear-length.	Weight.	Age.
	<i>mm.</i>	<i>gms.</i>	
Parents:			
♀ 438.....	184	2,550	20 weeks.
♂ 437.....	177	2,510	Do.
Mid-parental....	180.5	2,530	
Offspring:			
♂ 719.....	180	1,970	20 weeks.
♀ 720.....	185	2,030	Do.
♂ 721.....	180	2,010	Do.
♂ 725.....	176	1,825	Do.

Another cross 6 mating was obtained between ♀ 247 and ♂ 248 (produced in cross 1). The character of the young is shown in table 11.

TABLE 11.

	Ear-length.	Weight.	Age.
	<i>mm.</i>	<i>gms.</i>	
Parents:			
♀ 247.....	152	3,290	Adult.
♂ 248.....	153	3,930	Do.
Mid-parental....	152.5	3,610	Do.
Offspring:			
♀ 397.....	122	1,375	19 weeks.
♂ 398.....	130	1,770	Do.
♀ 400.....	135	2,460	8 months.
♀ 401.....	135	1,860	19 weeks.
♂ 402.....	130	1,755	Do.

Contrary to the result shown in table 9, the young obtained from this mating all fall short of the mid-parental ear-length by from 17 to 29.5 mm., indicating probably conditions of nutrition below the normal, during the period of principal growth of the ears, or of the transmission by the parents of a condition of ear-length inferior to that which they mani-



tested. The young vary in normal fashion about a mean ear-length of 130.4 mm. The total range is only 13 mm., indicating no Mendelian heterogeneity among the gametes produced by the parents, though both were  $F_2$  half-lops.

One of the young produced in this litter (♀ 400) was mated with the lop-eared ♂ 179, table 2. The result is shown in table 12. Six offspring were obtained from this mating; they vary rather closely about the mid-parental ear-length, though chiefly below it, as we might expect from the fact that the mid-parental value given is based upon measurements of adults, and that of the young upon measurements at the age of 20 weeks. The total range of variation is 15 mm.

TABLE 12.

	Ear-length.	Weight.	Age.
	<i>mm.</i>	<i>gms.</i>	
Parents:			
♀ 400.....	135	2,460	8 months.
♂ 179.....	210	3,410	Adult.
Mid-parental....	172.5	2,935	
Offspring:			
♂ 703.....	162	1,680	20 weeks.
♂ 704.....	166	1,670	Do.
♀ 705.....	160	1,520	Do.
♂ 706.....	171	1,880	Do.
♀ 707.....	160	1,715	Do.
♀ 708.....	175	1,720	Do.

Female 400 was likewise mated with her father (♂ 248), producing a litter of 4 young, all of which fell below the mid-parental ear-lengths. (See table 13.)

TABLE 13.

	Ear-length.	Weight.	Age.
	<i>mm.</i>	<i>gms.</i>	
Parents:			
♀ 400.....	135	2,960	8 months.
♂ 248.....	153	2,930	Adult.
Mid-parental....	144	3,445	
Offspring:			
♀ 818.....	135	1,500	20 weeks.
♂ 819.....	137	1,710	Do.
♀ 820.....	128	1,780	Do.
♀ 821.....	126	1,560	Do.

The deviations are -9, -7, -16, and -18, average -12.5 mm. But the total range of variation is only 11 mm., or scarcely greater than that observed among short-eared rabbits. Certainly this result affords no evidence of heterogeneity as regards ear-character among the gametes formed by the parents, though one was an  $F_1$  and the other an  $F_2$  cross-bred between the lop-eared and the short-eared races.

## OTHER MATINGS OF HALF-BLOOD LOPS AND ADDITIONAL CROSS 6 MATINGS.

Other matings in which the rabbits ♀ 247 and ♂ 248 were concerned are recorded in tables 14 and 15.

In mating 1 (with ♂ 179) ♀ 247 gave a fully normal blending result. Of the 5 young produced, 2 surpassed the mid-parental ear-length, 1 equaled it, and 2 fell below it. All were intermediate, and the range of variation was 14 mm., or about one-fourth of the difference between the parents. In mating 2 (with ♂ 319) ♀ 247 gave a result similar to that which she had given with ♂ 248. All the young were intermediate in ear-length, but all fell short of the mid-parental ear-length, by from 3 to 16 mm. This was not due to consanguinity, for ♀ 247 and ♂ 319 were not closely related. It may, however, have been due to inferior conditions of nutrition, perhaps resulting from the large size of the litter. The whole litter seems to have been affected alike, the total range of variation among the seven young being only 11 mm.

TABLE 14.

MATING 1.				MATING 2.			
	Ear-length.	Weight.	Age.		Ear-length.	Weight.	Age.
Parents:	<i>mm.</i>	<i>gms.</i>		Parents:	<i>mm.</i>	<i>gms.</i>	
♀ 247 .....	152	3,290	Adult.	♀ 247.....	152	3,290	Adult.
♂ 179 .....	210	3,410	Do.	♂ 319.....	200	3,955	Do.
Mid-parental	181	3,350	Do.	Mid-parental	176	3,622	Do.
Offspring:				Offspring:			
♀ 635 .....	170	1,740	20 weeks.	♀ 731.....	170	1,970	20 weeks.
♀ 636 .....	183	1,620	19 weeks.	♀ 732.....	170	2,100	Do.
♀ 637 .....	180	1,990	20 weeks.	♀ 733.....	160	2,020	Do.
♂ 638 .....	170	1,630	20 weeks.	♀ 734.....	173	1,710	Do.
♂ 639 .....	184	1,505	20 weeks.	♂ 736.....	165	1,785	Do.
				♂ 737.....	160	1,700	Do.
				♀ 738.....	171	2,020	Do.

Male 248 was mated with three different short-eared females, none of which was nearly related to him. The results are shown in table 15.

In mating 1, ♂ 248 gives a result like that which he had given when mated with his sister (♀ 247). All but 1 of the 6 young fell below the mid-parental ear-length by from 8 to 19 mm. The shortest-eared one had exactly the same ear-length (115 mm.) as the short-eared parent, a result unparalleled elsewhere in these experiments except in one case, presently to be noticed. The shortness in this case can not be attributed to the poor condition or small size of the individual, for it was the largest rabbit but one in the litter, a position which it maintained throughout the growth period. Apparently this individual represents an extreme variate of a fluctuating group. The extreme range of variation in this litter was 23 mm.; the difference between the parents, 38 mm.



Mating 2 shows a result more nearly normal. Two individuals exceed the mid-parental ear-length by 3 mm., 2 fall short of it 7 mm., and 1 by 9 mm. The total range of variation is 12 mm.

In mating 3, which produced 2 litters of young, the variations are again chiefly below the mid-parental ear-length, but to no greater extent than we might expect, in view of the difference in age between parents and children, when measured. In litter 1 the deviations are -2, +3, -4, and -2 mm., a nearly normal result; but in litter 2, four individuals show a deviation of -7 mm., and one a deviation of +3 mm. The range in litter 1 is 7 mm.; in litter 2, 10 mm. There is no evidence of heterogeneity among the gametes.

TABLE 15.

MATING 1.				MATING 3.			
	Ear-length.	Weight.	Age.		Ear-length.	Weight.	Age.
	<i>mm.</i>	<i>gms.</i>			<i>mm.</i>	<i>gms.</i>	
Parents:				Parents:			
♀ 255 .....	115	2,650	Adult.	♀ 389 .....	105	2,090 <sup>1</sup>	Adult.
♂ 248 .....	153	3,930	Do.	♂ 248 .....	153	3,930	Do.
Mid-parental	134	3,290	Do.	Mid-parental	129	....	Do.
Offspring:				Offspring:			
♀ 619 .....	125	1,820	19 weeks.	Litter 1 —			
♀ 620 .....	120	1,750	20 weeks.	♀ 653 .....	127	1,465	20 weeks.
♂ 621 .....	138	1,700	Do.	♀ 654 .....	132	1,845	Do.
♀ 622 .....	115	1,885	Do.	♀ 655 .....	125	1,840	Do.
♂ 624 .....	126	1,720	19 weeks.	♀ 656 .....	127	1,745	Do.
♂ 625 .....	125	1,910	20 weeks.	Litter 2 —			
MATING 2.				♂ 793 .....	120	1,700	20 weeks.
Parents:				♀ 794 .....	120	1,740	Do.
♀ 269 .....	92	1,935	Adult.	♀ 795 .....	120	1,860	Do.
♂ 248 .....	153	3,930	Do.	♂ 796 .....	130	1,690	Do.
Mid-parental	122	2,932	Do.	♂ 797 .....	120	1,770	Do.
Offspring:							
♀ 726 .....	115	1,730	20 weeks.				
♀ 727 .....	113	1,685	Do.				
♂ 728 .....	115	1,695	Do.				
♂ 729 .....	125	1,500	Do.				
♀ 730 .....	125	1,930	Do.				

<sup>1</sup> At 20 weeks.

Some other matings which fall in the category of cross 6, and constitute a second generation ( $F_2$ ) from cross 3, are included in table 16.

The statistics contained in table 16 are not very satisfactory because the observations are made at such different ages, and because, in one case at least, that of ♂ 381, a remarkable increase in ear-length is recorded subsequent to the age of 18 weeks. For observations made at the same age, however, the variability in ear-length is considerable. The range of variation in mating 1, litter 1, is 17 mm.; in litter 2 it is 15 mm.; in mating 2, it is 18 mm. In generation  $F_1$ , cross 3, the range of variation was only

slightly less, viz, 14 mm. So far, then, as table 16 is concerned, we get no clear evidence of heterogeneity among the gametes formed by the cross-breds produced by cross 3.

TABLE 16.

MATING 1.				MATING 2.			
	Ear-length.	Weight.	Age.		Ear-length.	Weight.	Age.
Parents:	<i>mm.</i>	<i>gms.</i>		Parents:	<i>mm.</i>	<i>gms.</i>	
♀ 175 (pl. 3, fig. 10) ...	170	4,305	Adult.	♀ 178 .....	170	4,070	Adult.
♂ 176 .....	166	4,130	Do.	♂ 176 .....	166	4,130	Do.
Mid-parental	168	4,218	Do.	Mid-parental	168	4,100	Do.
Offspring:				Offspring:			
Litter 1 —				♀ 471 .....	147	1,470	17 weeks.
♂ 375 .....	160 <sup>1</sup>	2,960	6 months.	♀ 472 .....	168	1,865	Do.
♂ 376 .....	172 <sup>1</sup>	2,975	Do.	♂ 474 .....	163	1,733	Do.
♂ 381 (pl. 3, fig. 12) ...	{ 155 <sup>1</sup>	2,800	22 weeks.	♀ 475 .....	150	1,515	Do.
	{ ..... 3,125	6 months.		♀ 476 .....	150	1,750	Do.
	{ 168	3,800	1 year.	♂ 480 .....	150	1,610	15 weeks.
Litter 2 —							
♂ 759 .....	180	2,220	20 weeks.				
♂ 760 .....	170	2,200	Do.				
♀ 761 .....	185	2,410	Do.				

1 18 weeks.

The female half-blood lop 175 (plate 3, fig. 10) produced by cross 3 was mated with the three-quarter-blood lop ♂ 437 (cross 5), and produced a litter of 5 young, the character of which is shown in table 17.

TABLE 17.

	Ear-length.	Weight.	Age.
Parents:	<i>mm.</i>	<i>gms.</i>	
♀ 175 .....	170	4,305	Adult.
♂ 437 .....	{ 184	2,550	20 weeks.
	{ 200	3,140	30 weeks.
Mid-parental ....	185	3,722	Adult.
Offspring:			
♀ 847 .....	176	1,920	18 weeks.
♀ 848 .....	188	1,800	17 weeks.
♀ 849 .....	180	1,970	Do.
♂ 851 .....	174	1,750	16 weeks.
♂ 852 .....	190	1,790	18 weeks.

These young early (16 to 18 weeks) attained a large size, indicating conditions favorable for growth. In ear-length they fluctuated about the mid-parental condition, which was exceeded by 2 individuals, while 3 fell short of it. All had ear-lengths intermediate between those of their respective parents. The range of variation among them at 18 weeks was 14 mm., exactly the same as in cross 3, from which the mother was derived. The greatest deviations from the mid-parental were -11 (at 16 weeks) and +5 (at 18 weeks). No evidence is afforded of unusual

heterogeneity among the gametes of either parent, although both were cross-bred individuals.

Females 175 and 178 (cross 3) were also used in back-crosses with a lop-eared male (179), resulting in the production of three-quarter-blood lops. The character of these young is shown in table 18.

TABLE 18.

MATING 1.				MATING 2.			
	Ear-length.	Weight.	Age.		Ear-length.	Weight.	Age.
	<i>mm.</i>	<i>gms.</i>			<i>mm.</i>	<i>gms.</i>	
Parents:				Parents:			
♀ 175 .....	170	4,305	Adult.	♀ 178 .....	170	4,070	Adult.
♂ 179 .....	210	3,410	Do.	♂ 179 .....	210	3,410	Do.
Mid-parental	190	3,857	Do.	Mid-parental	190	3,740	Do.
Offspring:				Offspring:			
♀ 487 .....	182	2,740	6 months.	♀ 546 .....	190	2,242	20 weeks.
♂ 491 .....	182	1,795	16 weeks.	♀ 547 .....	185	3,160	26 weeks.
♂ 492 .....	190	2,035	Do.	♂ 548 .....	195	2,320	19 weeks.
♂ 493 .....	200	3,330	Adult.	♀ 549 .....	193	2,900	26 weeks.
	170	1,900	16 weeks.	♀ 550 .....	200	2,460	Do.
				♀ 552 .....	185	2,360	Do.

The data for mating 1 are incomplete; but those recorded for mating 2 are entirely satisfactory. They show a total range of variation in ear-length at 26 weeks of 15 mm. which is very similar to that found in cross 3, by which the mother was produced. The greatest minus deviation from the mid-parental ear-length is 5 mm.; the greatest plus deviation, 10 mm.; the average deviation, 4.6 mm. The nearest approximation to the short-eared parent is 15 mm., to the long-eared parent 10 mm. The inheritance may fairly be described as blending, with no evidence of segregation in  $F_2$ .

The half-blood lop ♂ 176 was also employed in a back-cross with his mother, the Belgian hare, ♀ 431 (plate 3, fig. 9). Table 19 shows the result obtained.

TABLE 19.

	Ear-length.	Weight.	Age.
	<i>mm.</i>	<i>gms.</i>	
Parents:			
♀ 431 .....	118	3,400	Adult.
♂ 176 .....	166	4,130	Do.
Mid-parental .....	142	3,765	Do.
Offspring:			
♂ 520 .....	145	2,660	27 weeks.
♀ 521 .....	142	2,875	Do.
♂ 522 .....	135	2,520	Do.
♀ 523 .....	135	2,690	Do.
♀ 524 .....	128	2,180	Do.
Average .....	137	2,581	

The offspring fluctuate in ear-length about the mid-parental condition; 2 of them exceed it, 3 fall short of it. The minus deviations, however, are greater than the plus ones, precisely as in lop-eared rabbits bred *inter se* (p. 17). The range of variation is 17 mm., which is greater than that occurring among short-eared rabbits, but less than that occurring among lop-eared rabbits.

Another son of ♀ 431, own brother to ♂ 176, was likewise mated with his mother. This male (177, cross 3) had ears 10 mm. shorter than those of his brother (♂ 176). The mid-parental ear-length, accordingly, was only 137 mm. Two young only were reared to an age of 20 weeks, and each of them had an ear-length of 125 mm.

Further tests of the half-blood lop females 175 and 178 are afforded by the crosses recorded in table 20, with a related three-quarter-blood lop male (319) produced by cross 4.

TABLE 20.

MATING 1.				MATING 2.			
	Ear-length.	Weight.	Age.		Ear-length.	Weight.	Age.
	mm.	gms.			mm.	gms.	
Parents:				Parents:			
♀ 175 .....	170	4,305	Adult.	♀ 178 .....	170	4,070	Adult.
♂ 319 .....	200	3,955	Do.	♂ 319 .....	200	3,955	Do.
Mid-parental	185	4,130	Do.	Mid-parental	185	4,012	Do.
Offspring:				Offspring:			
♀ 674 .....	185	2,400	20 weeks.	Litter 1 —			
♂ 675 .....	175	2,350	Do.	♀ 660 .....	195	2,100	20 weeks.
♂ 677 .....	192	2,410	Do.	♂ 661 .....	191	2,750	Do.
♂ 678 .....	180	1,420	Do.	Litter 2 —			
				♂ 754 .....	150	1,460	19 weeks.
				♂ 755 .....	162	1,860	18 weeks.

The young produced by mating 1 are all intermediate in ear-length between their parents. One (♀ 674) exactly attains at 20 weeks of age the mid-parental ear-length, a second (♂ 678) would doubtless have done so had he not fallen into bad condition at about 13 weeks of age. Previous to that he had been one of the largest and longest-eared rabbits in the litter. Of the remaining 2, both of which developed normally and were of large size at 20 weeks of age, one exceeded the mid-parental ear-length by 7 mm. and the other fell 10 mm. short of it, approaching to within 5 mm. of the ear-length of the short-eared parent. The range of variation (17 mm.) is not excessive, and the result may be described as a fully normal blend, with no indication of heterogeneity among the gametes of the cross-bred parents.

Mating 2 yielded 2 litters very different in character and illustrating rather strikingly the influence of external conditions on growth. Litter 1 consisted of 2 young only. They were born in summer and developed under optimum conditions as regards food supply. At 20 weeks of age they had attained large size and had ear-lengths exceeding by 6 and 10

mm. respectively the mid-parental ear-length. Litter 2, on the other hand, was born in the winter. It consisted originally of 8 individuals. The 2 weakest ones in the litter died, one previous to, the other subsequent to weaning. The 4 largest ones were stolen, leaving 2 survivors, ♂ 754 and ♂ 755, both of which when last measured gave evidence of having been permanently stunted in size and ear-length by the hard conditions under which they had developed. They are too abnormal to throw any light on the inheritance of ear-length in this cross.

#### MATINGS OF THREE-QUARTER-BLOOD LOPS.

The male 319, employed in the matings last described, was also used in crosses with short-eared rabbits and with a three-quarter-blood lop, his sister. The results of the crosses with short-eared females are shown in table 21.

TABLE 21.

MATING 1.				MATING 2.			
	Ear-length.	Weight.	Age.		Ear-length.	Weight.	Age.
Parents:	mm.	gms.		Parents:	mm.	gms.	
♀ 268 .....	105	2,280	Adult.	♀ 105 .....	100	....	9 months.
♂ 319 .....	200	3,955	Do.	♂ 319 .....	200	3,955	Adult.
Mid-parental	152	3,117	Do.	Mid-parental	150	....	Do.
Offspring:				Offspring:			
Litter 1 —				♀ 743 .....	150	1,900	20 weeks.
♂ 657 .....	155	2,530	20 weeks.	♂ 744 .....	148	2,170	Do.
♀ 658 .....	151	2,460	Do.	♂ 745 .....	145	1,990	Do.
♂ 659 .....	156	2,450	Do.	♀ 745A .....	148	1,840	Do.
Litter 2 —				♂ 746 .....	145	1,990	Do.
♂ 662 .....	141	1,980	20 weeks.	♂ 746A .....	147	1,900	Do.
♀ 663 .....	142	1,690	Do.				
♂ 664 .....	160	2,200	Do.				
♀ 665 .....	141	1,575	Do.				

The 7 young produced by mating 1 fluctuate about the mid-parental condition of ear-length. The greatest minus variation is 11 mm., the greatest plus variation 8 mm., giving a total range of variation of 19 mm. This is not large, considering that the difference between the parents is 95 mm. The greatest deviation from the mid-parental, 11 mm., is 36 mm. removed from the nearest parental ear-length, that is, it is less than one-third as great as the least deviation from either parent. The inheritance is unmistakably blending. Even more clearly is this the case in mating 2. The parents differ in ear-length by 100 mm. The young are all almost exactly intermediate. The entire range of variation in the 6 young is only 5 mm., while the nearest approximation to the ear-length of either parent is nine times this amount. A better example of fully blending inheritance can scarcely be imagined. In neither mating do we get evidence of heterogeneity among the gametes formed by the three-quarter-blood father (♂ 319).



It is of interest to note that both the mothers employed in matings 1 and 2 were employed also in cross 2, with the lop ♂ 179. In that case, also, they gave a distinctly and fairly uniform blending result.

Male 319 was mated also with his sister (♀ 322), producing a litter of only 2 young. These closely resembled their parents in ear-character. (See table 22.)

TABLE 22.

	Ear-length.	Weight.	Age.
	<i>mm.</i>	<i>gms.</i>	
Parents:			
♀ 322.....	195	4,450	Adult.
♂ 319.....	200	3,955	Do.
Mid-parental....	197.5	4,202	Do.
Offspring:			
♀ 779.....	208	2,680	20 weeks.
♀ 780.....	190	1,950	16 weeks.

The latest measurement recorded for one of them (♀ 780) was made at 16 weeks of age, but already she had attained an ear-length of 190 mm. At maturity she would doubtless have equaled or exceeded the mid-parental ear-length. The other one (♀ 779) did exceed the mid-parental ear-length at 20 weeks of age by more than 10 mm., and she exceeded by 8 mm. the ear-length of the long-eared parent. Her size also at 20 weeks of age was very large, viz, 2,680 grams. This unusually great plus variation was doubtless due in part to extremely favorable conditions during the growth period, especially during the period of lactation. During that period the mother's milk was divided among 3 young only, but 1 of these died soon after the young were weaned. At the last measurement recorded, its ear-length was a little less than that of ♀ 780, while in size it was inferior to both ♀ 779 and ♀ 780.

TABLE 23.

	Ear-length.	Weight.	Age.
	<i>mm.</i>	<i>gms.</i>	
Parents:			
♀ 322.....	195	4,450	Adult.
♂ 179.....	210	3,410	Do.
Mid-parental....	202.5	3,930	Do.
Offspring:			
♀ 589.....	{ 205	2,460	20 weeks.
	{ 210	2,785	25 weeks.
	{ 200	2,220	20 weeks.
♀ 590.....	{ 205	2,510	25 weeks.
	{ 195	1,970	20 weeks.
♂ 591.....	{ 200	2,865	33 weeks.
	{ 190	2,080	20 weeks.
♀ 592.....	{ 195	2,235	25 weeks.

The same three-quarter-blood female (322) which was mated with ♂ 319 (table 22) was mated also with the lop ♂ 179, producing a litter of seven-eighth-blood lops. (See table 23.) Two of the 4 young reared had

at 25 weeks of age ear-lengths identical with those of the respective parents, viz, of 195 and 210 mm. The other two had intermediate ear-lengths of 200 and 205 mm. respectively. This is a fully normal blending result. The total range of variation is 15 mm. In both ear-length and size the young are similar to those produced by the mating with ♂ 319 (table 22).

CROSS 7.—QUARTER-BLOOD LOP FEMALE × SHORT-EARED MALE.

Three different quarter-blood lop females, 521, 522, and 524 (table 18), produced by a mating of the Belgian hare with her son (♂ 176), were mated with a son of the same Belgian hare by an unrelated short-eared male. (See table 14.) The outcome of these matings is shown in table 24.

TABLE 24.

MATING 1.				MATING 3.			
	Ear-length.	Weight.	Age.		Ear-length.	Weight.	Age.
	<i>mm.</i>	<i>gms.</i>			<i>mm.</i>	<i>gms.</i>	
Parents:				Parents:			
♀ 521 .....	142	2,875	27 weeks.	♀ 524 .....	128	2,160	27 weeks.
♂ 235 .....	110	2,945	Adult.	♂ 235 .....	110	2,945	Adult.
Mid-parental	126	2,910		Mid-parental	119	2,552	
Offspring:				Offspring:			
♂ 809 .....	135	2,080	20 weeks.	♂ 834 .....	115	1,600	20 weeks.
♂ 810 .....	125	1,800	Do.	♂ 835 .....	125	1,700	Do.
♀ 811 .....	120	1,820	Do.	♀ 836 .....	121	1,820	Do.
♀ 813 .....	115	2,035	Do.	♀ 837 .....	116	1,450	Do.
♂ 814 .....	125	1,960	Do.	♀ 838 .....	134	2,000	Do.
♀ 815 .....	126	2,150	Do.				
MATING 2.							
Parents:							
♀ 522 .....	135	2,520	27 weeks.				
♂ 235 .....	110	2,945	Adult.				
Mid-parental	122.5	2,732					
Offspring:							
♀ 823 .....	125	2,300	20 weeks.				
♂ 824 .....	125	2,250	Do.				

The offspring show, as regards ear-length, a rather wide range of variation, 20 mm., which is nearly two-thirds of the difference in ear-length between the parents. The average ear-length of the offspring corresponds, in each litter, closely with the mid-parental ear-length, the plus and minus deviations being, except in mating 3, about equal in number and amount. In mating 1, 3 of the 6 young have approximately the mid-parental ear-length, but 2 show minus deviations of 6 and 11 mm. respectively, and 1 shows a plus deviation of 9 mm.

The 2 young produced by mating 2 were of large size at 20 weeks of age, indicating conditions of nutrition above the average. The ear-length of each exceeds by 2.5 mm. the mid-parental ear-length.

The 5 young produced by mating 3 show 2 minus deviations of 3 and 4 mm. respectively, and 3 plus deviations of 2, 6, and 15 mm. respectively.

CROSS 8. — QUARTER-BLOOD LOP  $\times$  THREE-QUARTER-BLOOD LOP.

A single mating of this sort produced a litter of 3 young, all very similar and close to the mid-parental ear-length. (See table 25.) The observations were discontinued when the young were 14 or 16 weeks old, but the mid-parental ear-length of the parents, when they were 20 weeks old, had already been closely approximated. The deviations were  $-2$ ,  $-5$ , and  $-5$  mm. If growth progressed normally from the age of 14 or 16 weeks on, they would surely have attained the adult mid-parental ear-length, viz, 167.5 mm.

TABLE 25.

	Ear-length.	Weight.	Age.
	<i>mm.</i>	<i>gms.</i>	
Parents:			
♀ 523.....	{ 130	1,930	20 weeks.
	{ 135	2,690	27 weeks.
♂ 492.....	{ 195	2,540	20 weeks.
	{ 200	3,330	43 weeks.
Mid-parental....	{ 162.5	2,235	20 weeks.
	{ 167.5	3,010	Nearly grown.
Offspring:			
884.....	160	1,450	14 weeks.
885.....	157	1,300	14 weeks.
886.....	157	1,450	16 weeks.

## LIMITATIONS OF THE DATA STUDIED.

In attempting to draw conclusions from the statistics presented in the foregoing pages, one must bear in mind certain of their limitations and imperfections.

(1) Ear-length is modified to some extent by external conditions. If the young rabbit is well nourished up to the age of 20 weeks, its ear-length will be greater than if it is poorly nourished, other conditions being equal. While we have attempted to give our rabbits the best of care at all seasons, it is inevitable that the quality of food supplied at different seasons of the year should vary, and with variation in the quality of the food goes variation in the growth rate. This renders it difficult to compare with each other, as regards ear-character, rabbits reared at different seasons of the year. But it has been impossible for us to rear enough rabbits at any one season to afford adequate material for comparisons. Hence we are forced to utilize material produced at different seasons of the year.

(2) Size of litter is of some consequence in determining the growth rate of a rabbit. If there are several young in a litter each gets a smaller amount of food during the period of lactation than it would have received had the litter been smaller. Our material, however, is not extensive enough to allow us to institute comparisons merely between litters of substantially the same size.



(3) It is the belief of fanciers that a warm, moist atmosphere, during the period of active growth of the ears, favors the attainment of large ear-size. This view we have not been able to put to an experimental test, but we are inclined to think that the temperature and humidity are much less important factors than abundant food supply.

(4) Rabbits of the small, short-eared races have a shorter growth period than the larger races. Their ears are more likely to be full-grown at 20 weeks of age than are those of lop-eared rabbits. Therefore, in comparing rabbits of different ancestry at the same age, say 20 weeks, one is in danger of underestimating the ear-length of the larger-sized rabbit.

(5) A cross between rabbits of entirely different races is likely to result in young of unusual vigor, which causes them to attain a greater weight and ear-length than the hereditary constitution of either race by itself would result in. This is illustrated notably in cross 3, page 20. Superior size or ear-length, induced by crossing, we should not expect to be permanent in later generations.

(6) Disease frequently interrupts the orderly progress of a growth-curve and necessitates the omission altogether of certain series of observations.

#### CONCLUSIONS.

Notwithstanding these limitations, which manifestly restrict the scope of our conclusions, certain generalizations are clearly justified.

(1) A cross between rabbits differing in ear-length produces offspring with ears of intermediate length, varying about the mean of the parental ear-lengths.

(2) It is immaterial whether the larger parent was father or mother; the result is the same in either case. As regards ear-length, then, we may say, reciprocal crosses give the same result. This shows that ear-size is a character inherited with equal intensity through father or mother.

(3) A study of the offspring of the primary cross-breds shows the blend of the parental characters to be permanent. No reappearance of the grand-parental ear-lengths occurs in generation  $F_2$ , nor are the individuals of that second generation as a rule more variable than those of the first generation of cross-breds. Fig. 3 shows the most extreme case of "scatter" in  $F_2$  that we have observed. Yet the variation in this case is no greater than among the young of lop-eared rabbits bred *inter se*.

(4) The extreme range of variation in ear-length among short-eared rabbits is about 10 mm.; in lop-eared rabbits it is two or three times as great, or from 20 to 30 mm. Among rabbits produced as crosses of various sorts between short-eared and lop-eared rabbits the range of variation in ear-length is mostly intermediate in amount.

(5) The form of the growth-curve for ear-length from the age of 2 weeks on is convex upward, indicating a steady diminution in the daily growth increment.



## PART II.—WEIGHT.

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Our statistics for size inheritance are not very satisfactory, because we were unable to keep any considerable number of rabbits until they were full grown, owing to the smallness of our breeding room, so that a large number of weighings of adults is not available for purposes of comparison. But the size of a growing rabbit varies greatly with the character of its food, and this in turn is dependent upon a variety of conditions which it was not possible for us fully to control. A comparison of the weights of growing rabbits at corresponding ages is, therefore, not altogether satisfactory, yet it is the best material we have.

In tables 1 to 25 the latest available weighing, or the heaviest weight, is recorded for each rabbit. But since the weighings there recorded were made at very different ages, it is necessary to select some particular age at which to make comparisons. The age of 18 weeks has been selected, because the weighings for that age are most numerous.

In table 26 are shown the average weights, at 18 weeks of age, of different lots of rabbits, each lot containing those of like ancestry. The number of individuals in each lot is also shown in the table, as well as the greatest range of variation in weight found in any litter of each lot. The statistics in table 26 are fullest for those crosses (left section) in which ordinary short-eared rabbits were concerned. The average weight of such rabbits, in a lot of 17 individuals, is seen to be 1,412 grams. For lop-eared rabbits it is something over 1,743 grams, the weight given in the table from observations on 2 rabbits. This weight, however, has been exceeded at 14 weeks of age by a majority of the lop-eared rabbits which we have reared, so that it is certainly too low.

The lots of rabbits, partly of short-eared, partly of lop-eared ancestry, have intermediate weights, the weight tending to increase with increase in the proportion of lop blood. The variability (range) in weight, which was found to be twice as great in lop-eared as in short-eared rabbits, is intermediate in the cross-bred lots, increasing with increase in the proportion of lop blood.

Both the position of the average for each lot, and the amount of variation within it, indicate that weight-inheritance, like the inheritance of ear-size, is blending in character. Neither dominance nor segregation in the Mendelian sense are recognizable.

The Belgian hare crosses and mixed crosses, recorded in the last sections of table 26, show, in general, results similar to those given by the crosses with short-eared rabbits, but many of the averages are less reliable

because based on too few individuals (in 4 cases, a single litter each time). The Belgian hare was heavier than the short-eared stock used, and it will be seen that, in all cases, her descendants exceed in size animals of the short-eared series having a like amount of lop blood. Further, a mixture of short and Belgian blood tends to produce a rabbit intermediate in weight between those of the short and of the Belgian series, respectively. (See table 26, right section.) All these observations confirm the idea that body-weight is a character blending in its inheritance.

TABLE 26. — *Size at 18 weeks of age of rabbits of different proportions of lop "blood," from crosses with short-eared, with the Belgian hare, or with both.*

Lop blood.	Short-eared.			Belgian hare.			Mixed.		
	Average weight.	Max. variation in weight.	Individuals observed.	Average weight.	Max. variation in weight.	Individuals observed.	Average weight.	Max. variation in weight.	Individuals observed.
	<i>gms.</i>	<i>gms.</i>		<i>gms.</i>	<i>gms.</i>		<i>gms.</i>	<i>gms.</i>	
None .....	1,412	315	17	.....	.....	.....	.....	.....	.....
One-eighth .....	.....	.....	.....	.....	.....	.....	1,791	490	13
One-fourth .....	1,592	345	20	1,788	627	5	1,580	205	4
Three-eighths .....	.....	.....	.....	.....	.....	.....	1,888	575	14
One-half:									
Gen. 1. ....	1,463	315	17	.....	.....	.....	.....	.....	.....
Gen. 2. ....	1,700	420	18	2,076	260	4	1,754	420	11
Both .....	1,585	420	35	.....	.....	.....	.....	.....	.....
Three-fourths:									
Gen. 1. ....	1,652	495	17	1,965	820	12	.....	.....	.....
Gen. 2. ....	.....	.....	.....	1,940	890	10	.....	.....	.....
Both .....	.....	.....	.....	1,954	890	22	.....	.....	.....
Seven-eighths .....	.....	.....	.....	1,936	590	4	.....	.....	.....
All .....	1,743 <sup>1</sup>	800 <sup>2</sup>	7	.....	.....	.....	.....	.....	.....

<sup>1</sup> This is certainly too low, for in litter 70, table 2, mating 3, it was surpassed by three of the five rabbits of the litter, already at 14 weeks of age. The average given (1,743) is for the two animals, ♂ 179 and ♀ 180 (table 2, mating 1).

<sup>2</sup> At 14 weeks.

When the parents differ in size, the young are clearly of intermediate size, but our observations are too incomplete to show in most cases whether the size is midway between that of the respective parents or not. Prof. W. C. Sabine has kindly pointed out that if linear dimensions give a mid-parental condition (the mean of the respective parental conditions), then we should expect the weights to be less than the mean of the parental weights, provided the proportions of parts are the same in all cases. But the proportions of the parts are different in the two parents, when rabbits of different size are mated with each other, and the proportions in the offspring are unmistakably intermediate between those of the respective parents.

This, perhaps, accounts for some of the peculiarities observed in comparing weights of the rabbit ♂ 248 with those of his parents, and with the mid-parental weights. All three rabbits were fully grown (2 or more years old) when the observations were made, and these are fairly complete. The maximum body-weight recorded for ♂ 248 was somewhat

in excess of the mid-parental (table 27), but since he shows a less percentage of bone to total body-weight than either parent it is probable that the excess is due in part at least to some temporary condition (fatness). If he showed a mid-parental percentage<sup>1</sup> of bone to body-weight, and this would possibly be the case if all 3 rabbits had been in like condition, as regards fatness, then his weight should be something less than the mid-parental weight, or about 3,326 grams, instead of the mid-parental weight (3,800) or the observed maximum weight (3,930). But in the absence of more extensive observations, we can not be certain that the percentage ratio of bone to body-weight is a mid-percentage. The question must remain an open one until further data can be accumulated.

TABLE 27. — *Relation between bone-weights and total body-weight in the rabbit ♂ 248 and in his parents.*

	Bone-weight.	Body-weight.	Per cent bone-weight.
	<i>gms.</i>	<i>gms.</i>	
Old ♀ lop .....	77.15	4,600	1.67
♂ 45 .....	39.35	3,000	1.31
Mid-parental .....	58.25	3,800	...
Son, ♂ 248 .....	49.7	3,930	1.26

As regards bone-size, however, we can reach more satisfactory conclusions, for this character is unaffected by temporary conditions of the flesh. In table 29 are recorded bone measurements of this family of rabbits, which show the measurements of the son (♂ 248) to be close to the mid-parental as regards both absolute measurements and proportions of parts.

In table 28 are recorded observations upon the weight and volume of certain bones of these same rabbits. Both in weight and in volume the bones of the son are less than the mid-parental. This is what we should expect if the bones of the son correspond with the mid-parental in linear dimensions and in the proportions of parts; for linear dimensions should be to each other about as the cube roots of the volumes and weights (provided the specific gravity is alike in all three cases).<sup>2</sup> On this hypothesis "expected weights" and "expected volumes" have been calculated for the son, and these are entered in table 28 in a parallel column, along with the observed weights and volumes. It will be noticed that the "expected" uniformly exceed the observed weights and volumes. The expected, to be sure, is less than the mid-parental, but the observed is still less. As regards the total weights of the parts observed, a graphic presentation is made in fig. 4 of the relation of mid-parental to expected and observed. The expected falls below the mid-parental by a certain amount, but the

<sup>1</sup> The percentages given are based upon the combined weights of particular bones, not of all the bones of the body.

<sup>2</sup> A comparison of the weights and volumes of corresponding bones in table 28 indicates that the specific gravity of the bones of the son (♂ 248) was slightly less than that of either parent, viz, about 1.19 for the son, 1.20 for the mother, and 1.26 for the father.



observed falls below the mid-parental by about three times that amount. It is in fact removed from the mid-parental only a little less than from the weight of the smaller parent. It is difficult to explain this extensive deviation, but it undoubtedly exists and is apparently fairly uniform, though possibly the method of computing the "expected" magnitudes is faulty. The computation is made in the following way. The cube root of the weight for each parent was found. These two roots were then added together, and their half-sum found, which was then cubed.

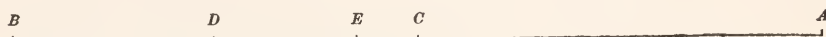


FIG. 4. Relation of the bone-weights of rabbit 248 to those of his parents and to the mid-parental bone-weights. If distances are laid off from a point at the left proportional to the bone-weights, they bear to each other the spacial relations of the following points: A, bone-weights of the mother; B, of the father; D, of the son, ♂ 248; C, the mid-parental; E, the expected bone-weights of the son.

Observed and expected deviate in the same sense from the mid-parental, that is, are less, but the uniform difference in amount between observed and expected is something requiring fuller analysis.

TABLE 28. — *Weights and volumes of skeletal parts of ♂ 248 in relation to those of his parents.*

[Mother, old female lop; father, ♂45; son, ♂248. Plate 1, figs. 2, 3, 1.]

Part.	Weights of bones (grams).							
	Mother.	Father.	Mid-parental.	Son.				
				Observed.	Expected.	Deviation of observed from expected.	Deviation of expected from mid-parental.	Deviation of observed from mid-parental.
Humerus . . . . .	5.9	3.2	4.55	3.7	4.4	-0.7	-0.1	-0.85
Femur . . . . .	10.8	5.9	8.35	7.5	7.8	-0.3	-0.5	-0.85
Tibia-fibula . . . .	9.1	5.45	7.27	6.15	7.13	-0.98	-0.14	-1.12
Innominate (of one side) . . . . .	8.4	4.1	6.25	5.4	5.9	-0.5	-0.35	-0.85
12 ribs (of one side)	6.95	3.2	5.07	3.9	4.7	-0.7	-0.3	-1.17
Vertebrae:								
1 to 6 . . . . .	7.4	3.3	5.35	4.6	5.04	-0.44	-0.31	-0.75
7 to 12 . . . . .	9.9	4.35	7.12	5.95	6.6	-0.65	-0.52	-1.17
13 to 20 . . . . .	18.7	9.85	14.27	12.5	13.7	-1.2	-0.5	-1.77
Total, 1 to 20.	36.0	17.5	26.75	23.05	25.5	-2.4	-1.25	-3.7
Total, counting weight of vertebrae once only.	77.15	39.35	58.24	49.7	55.43	5.58	2.64	8.54
Volumes of bones (cubic centimeters).								
Humerus . . . . .	5.2	2.5	3.85	3.1	3.65	-0.55	-0.20	-0.75
Femur . . . . .	9.1	5.0	7.05	6.5	6.94	-0.44	-0.11	-0.55
Tibia-fibula . . . .	7.1	4.0	5.55	5.0	5.40	-0.40	-0.15	-0.55

### PART III.—SKELETAL DIMENSIONS.

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Skeletons were prepared of certain of the rabbits concerned in this series of experiments, and upon these several series of measurements were made. The most complete series are recorded in tables 29 and 30.

In one case (cross 1, table 3) the skeletons of both parents were preserved, as well as that of one of the fully-grown young, viz, ♂ 248. The measurements of this animal (recorded in table 29) are approximately intermediate between those of his respective parents. They include 7 different skull measurements and 7 of other parts, chiefly bones of the appendages.

The skull of the lop-eared rabbit is relatively much longer and more slender than that of short-eared rabbits. (See plate 4.) The proportions of half-blood lops (like their absolute dimensions) are intermediate, corresponding closely with the mid-parental or mean of the parents in this respect. (See table 29, ratios.)

The limb bones are shorter in proportion to the length of the innominate bone in lop-eared than in short-eared rabbits. In this particular also part-blood lops are intermediate. (See tables 29 and 30, ratios.)

In the case of the rabbit ♂ 248, table 29, the deviation from the mid-parental measurements or proportions in no case equals one-fifth of the difference between the parents; in most instances it is much less. In this animal the inheritance of skeletal dimensions and proportions is unmistakably blending.

Measurements of another half-blood lop (♀ 167) are recorded in table 30. The mother's skeleton was not preserved. She was a short-eared rabbit similar to ♂ 45. If, then, the inheritance was blending also in the case of ♀ 167, her measurements and proportions should resemble those of ♂ 248, table 29. This, it will be observed, is the case.

Measurements of a third half-blood lop (♀ 178) are recorded in table 30. The father of this rabbit also was the old male lop, table 30. The mother was the Belgian hare (♀ 431, table 1A). In size and proportions of parts the Belgian hare occupied an intermediate position between the lop-eared and the small short-eared races used. Accordingly it is not surprising to find that the half-blood daughter (♀ 178) deviates from the other half-blood lops examined, both in absolute measurements and in proportions of parts, being more like lop-eared rabbits than they are.

A sister of ♀ 178, viz, ♀ 175 (table 5), had a son (♂ 492) by the lop-eared male 179. This last-named rabbit was a son of the old female lop whose skeletal measurements are recorded in table 29 and of the old male lop whose skull measurements are recorded in table 30. His own skeleton was not preserved, nor was the skeleton of ♀ 175 preserved, but if each was in skeletal character the mean of its parents, and if their son (♂ 492) was intermediate between them in character, we should expect his measurements to resemble the dimensions entered in column 4 of table 30. A comparison of this column with the next one shows that such was the case.

TABLE 29. — *Bone measurements of ♂ 248 and of his parents.*

Measurement.	Old female lop (mother).	♂45 (father).	Difference between parents.	Mean of parents.	♂248 (son).	Deviation from mean.	Per cent of dif. between parents.
	mm.	mm.	mm.	mm.	mm.	mm.	
1. Total length of skull . .	111.3	86.2	25.1	98.7	98.1	-0.6	2.6
2. Length, incisor to, palate inclusive . . . . .	51.8	36.	15.8	43.9	43.0	-0.9	5.7
3. Length, occipital to palate inclusive . . . .	73.0	57.8	15.2	65.4	63.0	-2.4	15.8
4. Width, anterior to orbit.	46.8	40.8	6.0	43.8	44.3	+0.5	8.3
5. Width, posterior to orbit	25.3	26.9	1.6	26.1	25.8	-0.3	18.8
6. Width, at auditory bullæ	39.8	34.0	5.8	36.9	36.7	-0.2	3.4
7. Length jugal arch . . .	43.9	37.2	9.7	42.1	42.8	+0.7	7.2
8. Length lower jaw . . . .	88.3	68.2	20.1	78.2	80.9	+2.7	13.4
9. Length femur . . . . .	95.8	85.	10.8	90.2	90.2	0	0
10. Length tibia . . . . .	116.4	98.1	18.3	107.2	108.7	+1.5	8.2
11. Length humerus . . . .	77.3	67.3	10.0	72.3	71.7	-0.6	6.0
12. Length ulna . . . . .	88.5	74.5	14.0	81.5	82.7	+1.2	8.6
13. Length radius . . . . .	74.0	62.5	11.5	68.2	67.8	-0.4	3.5
14. Length innominate . . .	103.0	81.7	21.3	92.3	92.3	0	0
Ratio:							
4 to 1 . . . . .	0.420	0.473	0.053	0.446	0.451	+0.005	9.4
5 to 1 . . . . .	.233	.315	.082	.274	.262	- .012	14.6
11 to 1 . . . . .	.694	.781	.087	.737	.731	- .006	6.9
13 to 1 . . . . .	.665	.725	.060	.695	.691	- .004	6.6
11 to 14 . . . . .	.750	.824	.074	.787	.777	- .010	13.5

A brother of ♀ 178, viz, ♂ 176 (table 5), was mated with the old female lop and had young which are described in table 6. One of these was the three-quarter-blood lop ♀ 504. Certain of her skeletal measurements are recorded in the last column but one of table 30. Her skull unfortunately was accidentally destroyed in preparation. If ♂ 176 had skeletal measurements like those of his sister (♀ 178) we should expect the daughter (♀ 504) to approximate the dimensions entered in column 6, table 30, which is the case. In fact, however, ♂ 176 had ears less long than those of his sister, and it is probable that his skeletal dimensions also were less, which would account for the fact that ♀ 504 falls somewhat below the skeletal dimensions given in table 30, column 6.



The measurements made upon the 2 three-quarter-blood lops (♂ 492 and ♀ 504) indicate that in their production, as in that of half-lops, the inheritance of skeletal dimensions is blending.

It would be premature to conclude that such is the case in all mammals. Farrabee (:05) has shown that in man hypophylangia (2-jointed fingers and toes) is associated with an abnormal shortness of the arms, legs, and trunk. It would seem that all the skeletal parts are abnormally shortened. Inheritance in this case is clearly not blending, but alternative. Some discontinuous alteration has evidently occurred in the growth-character of cells that form the skeleton, just as in the activities of the follicle cells in long-haired mammals (see Castle and Forbes, :06). It would be of interest to know whether such is the case also in bantam fowls and Shetland ponies.

TABLE 30. — *Bone measurements of rabbits.*

Measurement.	Old ♂ lop.	Half- blood lop ♀ 178.	Expected mean of ♂ 179 and ♂ 178.	Three- quarter- blood lop ♂ 492.	Mean of old ♀ lop (table 29) and ♀ 178.	Three- quarter- blood lop ♀ 504.	Half- blood lop ♀ 167.
	<i>mm.</i>	<i>mm.</i>	<i>mm.</i>	<i>mm.</i>	<i>mm.</i>	<i>mm.</i>	<i>mm.</i>
1. Total length of skull . .	103.7	104.5	106.0	107.5	....	....	98.5
2. Length, incisors to palate inclusive . . . . .	48.0	48.4	49.1	49.0	....	....	45.3
3. Length, occipital to palate inclusive . . . . .	67.4	66.5	68.3	68.6	....	....	63.4
4. Width, anterior to orbit.	46.3	45.4	46.6	47.4	....	....	43.4
5. Width, posterior to orbit	27.4	27.1	26.7	27.5	....	....	25.1
6. Width, at auditory bullae	36.4	37.0	38.1	39.6	....	....	35.9
7. Length jugal arch . . . .	45.9	....	....	46.0	....	....	41.7
8. Length lower jaw . . . .	....	87.6	....	86.4	87.9	84.0	....
9. Length femur . . . . .	....	99.0	....	100.	97.4	95.7	89.1
10. Length tibia . . . . .	....	....	....	119.6	....	109.0	105.1
11. Length humerus . . . . .	....	79.6	....	78.9	78.4	75.5	72.6
12. Length ulna . . . . .	....	90.2	....	91.8	89.3	88.0	81.7
13. Length radius . . . . .	....	75.9	....	76.7	74.9	73.5	68.0
14. Length innominate . . .	....	100	....	97.4	101.5	97.3	90.5
Ratio:							
4 to 1 . . . . .	0.446	0.435	0.440	0.441	....	....	0.443
5 to 1 . . . . .	.264	.259	.252	.248	....	....	.255
11 to 1 . . . . .	....	.761	....	.734	....	....	.737
13 to 1 . . . . .	....	.726	....	.713	....	....	.690
11 to 14 . . . . .	....	.796	....	.810	0.772	0.775	.802

Aside, however, from such unusual cases, it seems probable that skeletal dimensions, and so proportions of skeletal parts, behave in general as blending characters. The linear dimensions of the skeletal parts of an individual approximate closely the mid-parental dimensions.

Volume and weight magnitudes, however, follow a different law, which has not yet been clearly made out. It is plain that they are less than the mid-parental magnitude. (See Part II.)

It is probable that in plants, as well as in animals, linear dimensions are in general blending in their inheritance. In regard to the height of maize, Lock (:06, p. 130) says:

Some of the strains which were made use of were uniformly much taller than others. In  $F_1$  the height of the cross-breds between such strains was obviously intermediate. In a number of cases the cross was made between  $F_1$  plants and the shorter of the parental types. The offspring of this cross showed no such segregation into short and intermediate plants as was to be expected if Mendel's law held good. On the contrary, the plants produced were remarkably uniform in height.

This account agrees precisely with our observations upon the inheritance of linear dimensions in rabbits.

The obviously blending inheritance of height in this case does not contradict the known Mendelian behavior of the growth-habit in such plants as the sweet pea, where Bateson (confirming Mendel) has shown dwarfness to be alternative with tallness. Dwarfness is plainly such a discontinuous variation in plants as is hypophylangia in man, and its inheritance is quite different from that of ordinary variations in height. The former is a discontinuous variation, Mendelian in its inheritance; the latter belongs to a series of continuous variations, and is blending in its inheritance. In a dwarf plant the internodes are shortened throughout the entire plant, just as in a case of hypophylangia there is a general shortening of the skeletal parts.

## PART IV.—COLOR.

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### COLOR VARIATION IN RELATION TO COLOR FACTORS.

A preliminary discussion of color variation in the rabbit was made by Castle (:07*a*). Since that paper was written several obscure points have been cleared up. In the light of our present knowledge an attempt will be made to describe, in terms as simple as possible, the color varieties of rabbits and the mode of their production.

The gray pigmentation, common to wild rabbits, is complex in its nature, and all other color varieties are relatively simpler. The gray coat results from the joint action of several independent color factors; all other types of pigmentation result from a weakening or entire loss of one or other of the several factors concerned in producing a gray coat. In other words, color variation in the rabbit is wholly retrogressive. We are able to recognize the existence in the gray coat of the rabbit of 8 independent factors. To assume the existence of so many factors will probably seem to some absurd; at first it seemed so to us; but we have been forced step by step to the assumption that they exist as the simplest way of explaining the observed facts.

The factor hypothesis was first introduced by Cuénot (:03) to explain the latent transmission of pigment characters through albinos; it was developed independently by Tschermak (:03) to explain similar phenomena (kryptomerism, the existence of hidden factors) in beans; and has been further extended by Bateson (:06) and his associates.

The 8 color factors which are recognizable in the case of the gray rabbit, and the symbols which we shall use to designate them, are as follows:

- Symbol C. A common color factor necessary to the production of all pigment, wanting only in albinos.
- B. A factor for black, some substance which acting upon C produces black pigmentation.
- Br. A factor for brown, some substance which acting upon C produces a chocolate-brown pigmentation.
- Y. A factor for yellow, some substance which acting upon C produces yellow pigmentation.
- I. An intensity factor, which determines whether the pigmentation shall be intense (as in black and in yellow), dilute (as in blue and in cream), or of some intermediate degree of intensity.
- A. A pattern factor which causes the black or brown pigments to be excluded from certain portions of the individual

hairs, where yellow then shows. A "ticked" gray coat results. When this factor is present the under surfaces of the rabbit (tail, belly) are unpigmented (white). The symbol, A, stands for agouti, this factor having first been demonstrated in the "agouti" guinea-pig. (See Castle, :07.)

- U. A factor for uniformity of pigmentation (in distinction from spotting with white, S).
- E. A factor governing the extension of black and of brown pigmentation, but not of yellow. When most restricted in distribution the black or brown pigments are found in the eye and in the skin of the extremities only, but not in the hair, when more extended they occur also in the hair generally.

#### DEVELOPMENT OF THE FACTOR HYPOTHESIS.

Scientific hypotheses, to be of service, should be as simple as possible. Therefore no unnecessary assumptions should be made. To assume the existence in gray rabbits of eight independent color factors requires justification.

#### THE GENERAL COLOR FACTOR, C.

The existence of a color factor (C) was first suggested by Cuénot (:03) to explain how it is that albinos transmit in crosses the particular colors which were borne by their pigmented ancestors. This common color factor being acted upon by specific substances (perhaps color enzymes) produces specific pigments, such as black, brown, or yellow. No hypothesis simpler than this has been suggested, nor any other which adequately accounts for the observed facts.

#### THE SPECIFIC PIGMENT FACTORS, B, Br, AND Y.

The existence of separate factors for black and for brown pigmentation is shown beyond question by the results of crossing black with brown varieties, in guinea-pigs and in mice. In rabbits a brown variety is not known to us personally, though we have been informed that such a variety exists in continental Europe.

The existence of a separate factor (Y) for yellow pigmentation can scarcely be questioned, in view of the fact that the yellow pigmentation is as regards distribution quite independent of both black and brown, remaining extended throughout the fur when they are restricted to the eyes and the skin of the extremities.

#### THE INTENSITY FACTOR, I OR D.

The existence of an intensity factor was first announced by Bateson (:06) as having been demonstrated by Miss Durham in the case of mice.

For guinea-pigs and rabbits we are able to confirm completely Miss Durham's discovery. Since dilution or concentration of pigment is a

property transferable from one pigment (as black) to another (as yellow), it is evidently due either to some modification in C, or else to an independent factor. But it can not be due to C, since it is transmissible through an albino, which by hypothesis lacks C. We are forced to conclude that it is transmitted through some independent factor, which we shall designate I, intensity; it is alternative with D, a state of dilution (as in the blue modification of black, or the cream modification of yellow).

#### THE FACTOR FOR A PIGMENT PATTERN OF THE INDIVIDUAL HAIR, A.

Evidence for the existence of a factor (A) governing the pigment pattern of the individual hair has been presented elsewhere (Castle, :07a). It was first recognized in the case of the guinea-pig (Castle, :06) as an essential factor of the "agouti" coat, indeed as the only feature which differentiates the agouti variety from black. Hence the symbol A (agouti) was adopted to designate it. Cuénot (:04) employed the symbol G to designate in mice the agouti or gray coat, and designated black by a different symbol, but he failed to recognize that gray is simply black plus a second factor. Hence his G equals B (black) plus A. Hurst has independently discovered the existence of the A factor in rabbits (Proceedings Seventh International Zoological Congress, unpublished). In the guinea-pig, a new color variety, cinnamon-agouti, has been deliberately produced through the agency of the independent factor A. (See Castle, :08.)

#### THE FACTOR FOR UNIFORMITY OF PIGMENTATION, U, OR SPOTTING WITH WHITE, S.

The factor U (uniformity of pigmentation) is alternative with spotting with white, S. Its existence was first established by Cuénot (:04). Like I, the intensity factor, it may be regarded as a modifier of C, though not identical with it; for U and S are transmissible through albinos, which themselves have no pigmentation and which by hypothesis lack the factor C. U is also demonstrably independent of any particular color, for spotting with white is transferable in crosses from one color variety to another, as, for example, from black to yellow.

#### THE FACTOR FOR EXTENDED DISTRIBUTION OF BLACK OR BROWN, E, ALTERNATIVE WITH R (RESTRICTED DISTRIBUTION).

The assumed factor E is a modifier of black and brown, but not of yellow pigmentation. It is alternative to R, a restricted distribution of black and of brown pigments, in which distribution they are confined to the eyes and to the skin of the extremities. The distribution of yellow pigment (Y) is wholly unaffected by this factor. When black and brown are restricted, yellow remains as the principal or even as the exclusive pigmentation of the hair (yellow varieties).

That E really exists as an independent factor, and not as a condition merely of black or of brown, is shown by the following experiment. If one crosses a brown ("chocolate") guinea-pig with an ordinary yellow



one (black-eyed), the young are black pigmented, but in  $F_2$  4 varieties are obtained, viz, black, brown, black-eyed yellow, and brown-eyed yellow. The case, at first thought puzzling, is entirely plain if we consider the distribution independent of the kind of pigment. In the original cross extended brown was combined with restricted black. Extension dominated restriction, and black dominated brown, but in  $F_2$  black and brown each occurred both in the extended and in the restricted condition. Plainly the case is one of Mendelian dihybridism, in which two independent pairs of alternative characters are concerned.

The extension factor (E) may be replaced, not merely by the extreme condition (R) in which black and brown pigment are absent from the fur, but also by conditions of restriction less extreme, in which spots of black (or brown) occur on a background of yellow. Such intermediate conditions (E', E'', etc.) are heritable, and are alternative with E and R, respectively. In some of these intermediate conditions the spots are of large size and sharply limited, in others the spots are numerous and small. Each condition has a tendency to breed true, *i. e.*, is alternative to other conditions of E.

#### INTERRELATIONS OF FACTORS E AND U.

Spotting with black or brown on a yellow background is independent of spotting with white, though the two may coexist. The one is due to a modification of E, the other to a modification of U. When E and U are both unmodified the animal is of course black (or brown) pigmented all over. When U alone is modified (and occurs in condition S), the animal is black (or brown) but spotted with white. When E is modified (to E' or E'') but U is unmodified, the animal is spotted with black (or brown) on a yellow background, but is devoid of white. When both E and U are modified (to E' or E'' and to S, respectively) the animal bears two different sorts of colored spots on a white background. The spots are either black and yellow or brown and yellow, and constitute with the white background on which they lie the so-called "tricolor" condition, well known in the case of guinea-pigs, dogs, cats, and mice.

It is a singular fact that spots of black and of brown do not occur on the same animal, so a 4-colored condition is never attained. The reason for this is apparent, if the hypothesis stated in this paper is correct. The distribution of black and of brown is controlled by the same factors, E and S, so that when black and brown are present together, their distribution is the same, and black because of its greater opacity covers up the brown.

The "black-and-tan" dog is, we believe, an apparent, not a real, exception to this generalization; for the "tan" is not a chocolate-brown pigment such as is found in the brown water-spaniel, but merely a yellow pigment. The black-and-tan dog is not a spotted dog, but is a black dog plus a color-pattern, similar to the agouti-pattern of guinea-pigs and rabbits. In

this pattern black is largely excluded from the lower surfaces and from a spot over each eye, where yellow then shows. The correctness of this hypothesis is shown by the existence of this same pattern among brown-pigmented dogs. The brown-and-tan has chocolate-brown pigment above and tan (yellow) below, as well as a spot over each eye. It bears the same relation to self-brown that black-and-tan does to self-black. On this interpretation brown-and-tan is brown plus pattern, and black-and-tan is black plus pattern. If, then, brown-and-tan is crossed with self-black, black-and-tan offspring should result in  $F_1$ , and in  $F_2$  there should be obtained black-and-tan, brown-and-tan, self-black, and self-brown, in the proportions 9:3:3:1. The experiment is commended to dog breeders.

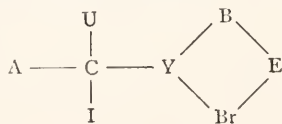
#### INTERRELATIONS OF FACTORS B, Br, AND Y.

Returning, after this digression, to a consideration of the interrelations of the three pigments, black, brown, and yellow, the fact seems clearly established that black and brown are closely related but alternative conditions dependent for their distribution upon two factors, which we may designate E and S, whereas yellow is dependent for its distribution solely upon one of these two factors, S. It would seem probable, therefore, that in the genesis of the hair pigments, yellow is a first product of the interaction of C and Y, which may or may not be further modified to produce brown or black, depending upon whether certain other factors (B and Br) are or are not present. The amount and distribution of the yellow pigment produced is conditioned by a factor which may assume phases U, S, S', etc. The amount of the yellow pigment which is converted into black or brown and its distribution is conditioned by another factor which may assume phases E, E', etc., to R.

#### GAMETIC STRUCTURE AND VARIATION.

A diagram like those employed by the organic chemist may help to show the relationships to each other of these 8 assumed pigment factors.

C, the general color factor, is indispensable to the manifestation of any of the others. All the others may be represented as linked directly or indirectly with it. E, however, is a modifier of B and Br alone, and is therefore joined with them alone in the diagram; and since B and Br are assumed to act only after Y has acted, they are represented as joined with it.



Homozygous gray rabbits, wild ones for example, possess and transmit all these 8 factors in each of their gametes. The diagram, therefore, expresses their gametic composition. A homozygous black rabbit lacks, of all these 8 factors, A alone. A yellow rabbit has R (restricted) in place of E (extended black or brown), but otherwise is like the gray, or else the

black rabbit. Those with A and those without A are, however, visibly different.

Theoretically, if each factor is capable of independent variation, 256 different gametic combinations should be possible. In reality we are acquainted with 18 visibly different color varieties, and we have evidence that 48 different gametic combinations are capable of realization. This leaves still a wide discrepancy between theoretical and known, and leads to the conclusion either that many as yet unknown mutations are possible in the rabbit, or that couplings may exist among these factors which prevent their independent action.

We have evidence of independent variation on the part of the factors A, C, I, U, and E, each of which has in one case or another either been lost or been replaced by the alternative condition already described; but B, Br, and Y are unvariable; at least we have not ourselves seen evidence among rabbits of independent variation on the part of these factors. There can be no question, however, that both in the guinea-pig and in the mouse such variation has occurred, resulting in the complete loss of B from the gamete, and it is possible, as elsewhere stated, that such a change has already occurred among European rabbits. Supposing, however, that B, Br, and Y are all constant constituents of the rabbit gamete and that each of the five others may be either present or absent, the number of different gametic combinations theoretically possible becomes 32. We have reason to believe that this entire assortment is produced and that 16 other ones also occur owing to a second and different sort of variation in factor C.

#### GAMETIC AND ZYGOTIC FORMULÆ.

The diagram given on page 49 was intended to express the known aggregate of independent factors which a pure gray rabbit transmits in each of its reproductive cells (gametes). In producing a new individual each reproductive cell must unite with another reproductive cell, the two together forming a zygote. An individual resulting from the union of two gametes of like constitution will be double as regards each hereditary factor. It is known as a homozygote (Bateson). This double condition we might express by a subscript<sub>2</sub> following the symbol for each factor indicated. We should then have a zygotic formula for the individual.

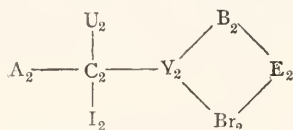
But it sometimes happens that a gamete unites with another gamete having a composition slightly different from its own—one which, for example, lacks one or more factors found in itself. The zygote produced is then a heterozygote and will be double as regards certain factors, but single as regards others. But in sexual reproduction, as is well known, there is a return from the double to the single condition. So that when a heterozygous individual attains sexual maturity, it forms gametes each of which contains the factor double in the zygote, but as regards those which were single in the zygote, half the time they will be present, half



the time absent from the gamete (or if not absent, then represented by an alternative condition). This is simply another way of stating the fundamental Mendelian principle that heterozygotes do not breed true, but form at least two different kinds of reproductive cells.

The breeder has to deal always with individuals, and only indirectly with gametes. Therefore zygotic formulæ are to him quite as important as gametic formulæ. Accordingly in what follows we shall endeavor to give the zygotic formula of each variety described. Its breeding capacity may quickly be inferred from an inspection of its zygotic formula. Each factor which is double in the zygote will be represented in every gamete formed, each factor which is single in the zygote will be present in only half the gametes formed, or will be represented by the alternative (recessive) condition expressed in the zygotic formula by a symbol in parenthesis.

The zygotic formula of a gray rabbit which breeds true (an ordinary wild one, for example) is  $B_2Br_2E_2A_2C_2I_2U_2Y_2$ , and the interrelations of these factors, as at present understood, may be expressed in a diagram.



Other gray rabbits are single (or heterozygous) as regards one or more of the factors enumerated in this formula, though none of them lacks altogether any one of these 8 factors. When a factor drops out altogether a new color variety is produced. New color varieties have undoubtedly originated in this way in the past, and are still doing so at the present time. A maturation division in which the two components of a double factor should fail to separate (as they do normally) might be the starting-point of a new color variety, since it would result in the production of a gamete which lacked a particular factor. Abnormal maturation divisions, therefore, may be the immediate cause of color variations.

#### COLOR VARIETIES OF THE RABBIT.

It is impossible to make a scientific classification of the color varieties of the rabbit without discarding or modifying some of the names now in use; for many of these names are either without significance or are misleading. From a perusal of the literature of the rabbit-fancy, we are unable to decide what certain named varieties are, and it is more than likely that we are not acquainted at first-hand with many varieties known to the fancy in Europe. All such cases must necessarily be omitted, for the present, from our classification.

For convenience we may recognize 4 general color types, viz, (1) gray, (2) black, (3) yellow, and (4) white. Each of the pigmented varieties

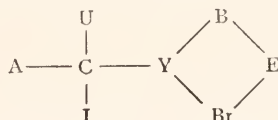
(gray, black, and yellow) may have either intense or dilute pigmentation (disregarding intermediate shades, which, however, exist and are heritable). Further, each may either have uniform pigmentation or be spotted with white (disregarding differences in the fineness of the spotting, which, however, exist and are heritable). Further, the yellow may have either pigmented or white under surfaces. Even with categories so inclusive as these, the number of visibly different pigmented varieties rises to 16, and since albinos may either have or not have pigmented extremities, the total number of visibly different varieties mounts to 18.

There is every reason to suppose that each of these 18 varieties may be obtained in a homozygous condition. Most of them, indeed, have been so obtained in our experiments. But for each homozygous condition there are possible several heterozygous conditions. An enumeration of all these is unnecessary, as the number is truly stupendous. With 5 independently variable characters (the number known to be independently variable in the rabbit) the number of different zygotic combinations theoretically possible is 243.

We shall content ourselves with enumerating the 18 different known gametic combinations, and in giving examples of a few of the different zygotic combinations.

#### GRAY TYPE.

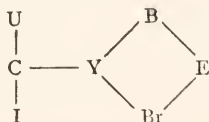
- (1) Gray, found in wild rabbits; gametic composition —



- (2) Blue-gray, same as the foregoing, with the substitution of D (dilute) for I (intense).  
 (3) Spotted gray, same as 1, with the substitution of S (spotted) for U (uniform pigmentation).  
 (4) Spotted blue-gray, same as 2, with the substitution of S for U.

#### BLACK TYPE.

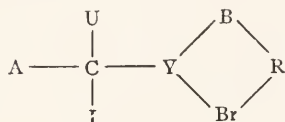
- (5) Black, same as 1 without A, namely,



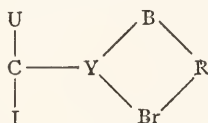
- (6) Blue (*i. e.*, dilute black), same as 5, with the substitution of D for I.  
 (7) Spotted black, same as 5, with the substitution of S for U.  
 (8) Spotted blue, same as 6, with the substitution of S for U.

YELLOW TYPE.

- (9) Yellow (with white belly and tail), same as 1, with R (restricted) substituted for E (extended black or brown pigmentation), namely,



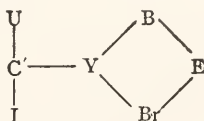
- (10) Cream (*i. e.*, dilute yellow), same as 9, with D substituted for I.  
 (11) Spotted yellow, same as 9, with S substituted for U.  
 (12) Spotted cream, same as 10, with S substituted for U.  
 (13) Sooty (yellow with pigmented belly and tail), same as 9 without A, or as 5 with R substituted for E, namely,



- (14) Pale sooty, same as 13, with D substituted for I.  
 (15) Spotted sooty, same as 13, with S substituted for U.  
 (16) Spotted pale sooty, same as 14, with S substituted for U.

WHITE TYPE.

- (17) White (wholly unpigmented), in any of the foregoing 16 varieties with C omitted.  
 (18) Himalayan white, a pink-eyed albino variety differing from 17 in appearance, in having black pigmented extremities (nose, ears, feet, and tail) and in having fur of a creamy white, not of a snowy white as in 17. Those with which we have experimented seemed to be of the formula<sup>1</sup> —



That is, they were black pigmented rabbits (see 5) in all points except C. It would seem that we must assume the presence of C in some form in an animal which like these does bear a certain amount of pigment. Nevertheless this C is not the same as the C found in dark-eyed pigmented varieties, for a cross of Himalayan with other albinos produces no dark-eyed offspring, and gives no increase of pigmentation over that found in the Himalayan parent, but rather a diminution of it (see Castle, :05). If, then, we assume C to be present in the Himalayan, it must be in a greatly modified form, as compared with its condition in dark-eyed animals. This is why we use C' rather than C in the formula. The factors E, I, and U, were all found to be present in our Himalayan rabbits, but not A, for crosses of Himalayan with homozygous gray gave only gray in

<sup>1</sup> April, 1909. Himalayan rabbits have now been produced which contain also factor A. They have extremities less heavily pigmented than ordinary Himalayans, and the tail is *white underneath*, as in gray and in yellow rabbits.

F<sub>1</sub>, and in F<sub>2</sub> gray, black, and Himalayan, but no other varieties. Whether it is possible to associate A with the other factors found in a Himalayan rabbit remains to be demonstrated.

The reader will naturally expect some concrete evidence in support of the gametic composition ascribed to the various color varieties in the foregoing enumeration. To a consideration of this we may proceed immediately. It would be wearisome to describe in detail all the experiments which have been made in the investigation of this matter. They have involved the production in various sorts of matings of some thousands of rabbits. It will suffice, we think, to cite from our experiments certain matings which were of such a nature as to test the validity of our hypothetical formulæ.

#### ZYGOTIC VARIATION WITHIN EACH COLOR VARIETY.

##### GRAY.

The formula has already been given of a gamete which transmits the coat characters of a wild gray rabbit. It contains, as we have seen, 8 distinct factors. Such a gamete might be produced by gray rabbits of many different sorts, all of which look alike but breed differently, *i. e.*, which have a different zygotic composition.

(1) The first sort which we will consider is homozygous (double) as regards each factor which enters into the composition of the gamete transmitting gray. Its zygotic formula is B<sub>2</sub>Br<sub>2</sub>E<sub>2</sub>A<sub>2</sub>C<sub>2</sub>I<sub>2</sub>U<sub>2</sub>Y<sub>2</sub> (compare diagram, p. 51). Every gamete which it forms transmits, therefore, all the components of a gray coat. This is the condition found in ordinary wild rabbits. One of our original stock of rabbits (♀ 431), a Belgian hare, was of this sort. In a variety of crosses she produced only gray offspring.

TABLE 31. — *Matings and young of ♀ 431, the Belgian hare.*

Mating.	Gray young.
With ♂ 56, an albino.....	5
With ♂ 8, a Himalayan albino .....	3
With old lop male, yellow.....	10
With ♂ 176, her son, gray .....	7
Total .....	25

The matings with ♂ 56 and ♂ 8 indicate that she did not carry albinism as a recessive character; the mating with the yellow rabbit shows that she did not carry yellow as a recessive character. The yellow rabbit in question was found by other tests to be heterozygous in the pattern factor A. Consequently the Belgian hare was almost certainly homozygous in that factor; otherwise half the young produced in this mating should have been black instead of gray.

(2) A second sort of gray rabbit produces (when mated with animals like itself) gray offspring and black ones, but produces none of other color varieties in any kind of mating. It differs from variety 1 only in regard to the factor A, in which it is heterozygous (single). Its zygotic formula accordingly is B<sub>2</sub>Br<sub>2</sub>E<sub>2</sub>AC<sub>2</sub>I<sub>2</sub>U<sub>2</sub>Y<sub>2</sub>. In half its gametes the A factor is transmitted along with all the other 7 factors; in half its gametes the factor A alone is wanting. Gray

rabbits of this sort are readily produced by mating a gray rabbit with a black one. A rabbit of this sort produced in a slightly different way was our gray ♂ 2005, which, when mated with a sooty yellow (♀ 1471), produced a litter of 3 black and 2 gray young; likewise our gray ♂ 2004, which, when mated with sooty yellow ♀ 1491, produced 5 black and 5 gray offspring (exactly the expected equality of blacks and grays). Many Belgian hares are of this second variety ("throwing blacks," as well as grays, but not other colors).

(3) A third sort of gray rabbit produces (when mated with animals like itself) albino offspring as well as gray ones, but none of other colors. It is heterozygous (single) in C, but otherwise homozygous. Its formula is  $B_2Br_2E_2A_2Cl_2U_2Y_2$ . We have at the present time some rabbits believed to be of this kind, but they are as yet not fully tested. Hurst (:05) also describes rabbits of this variety.

(4) A fourth sort of gray rabbit produces<sup>1</sup> young of the varieties gray, black, and white only. It is heterozygous (single) in A and C, but not in other factors. Its formula is  $B_2Br_2E_2ACl_2U_2Y_2$ . It is represented in our rabbits (♀ 1161 and ♂ 1172) produced by a cross between a white rabbit (of gray ancestry) and a heterozygous gray one. Mated with each other these two produced 17 young, distributed as follows: 10 gray, 3 black, and 4 white (expected 9:3:4). Male 1172 was mated also with a white female of black parentage (♀ 789), and produced 3 gray, 5 black, and 2 white offspring (expected 1:1:2).

Rabbits differing from variety 4 only in the respect that the albinos which they produce are of the Himalayan type are represented in our gray ♂ 48, and ♀ 49 and ♀ 50. They were produced by the mating of the Belgian hare ♀ 431 with a Himalayan (♂ 8). The result of their matings *inter se* is given in table 32.

TABLE 32. — *Matings and young of ♂ 48, gray.*

Matings.	Young.		
	Gray.	Black.	Himalayan.
With ♀ 49, gray .....	9	5	7
With ♀ 50, gray .....	15	5	6
Total <sup>1</sup> .....	24	10	13

<sup>1</sup> Expected ratio of 9:3:4, giving in this case 27:9:12.

The formula of such rabbits may be expressed by adding the symbol C' to the formula as given for variety 4, viz,  $B_2Br_2E_2AC(C')I_2U_2Y_2$ .

TABLE 33. — *Matings and young of gray ♀ 175.*

Mating.	Young.		
	Gray.	Yellow.	Black.
With ♂ 176, gray .....	24	13	0
With ♂ 177, gray .....	11	5	0
With ♂ 437½, gray .....	4	2	0
Total .....	39	20	0
Expected .....	3	1	0

(5) A fifth sort of gray rabbit produces young of the varieties gray and yellow, but none of other colors. It is heterozygous (single) in the extension factor E, carrying as an alternative (recessive) character R (restricted distribution of black and brown pigments). Its formula accordingly is  $B_2Br_2E(R)A_2C_2I_2U_2Y_2$ .

<sup>1</sup> When on this and subsequent pages the nature of the mating is not specified it will be understood that the mating is with animals of its own variety or of varieties recessive to its own.



It is represented in our gray ♂ 2071, which, when mated with a sooty yellow female (♀ 1414), produced 4 gray and 3 yellow young. This variety is represented likewise by ♀ 175 and ♂ 176, borne by the Belgian hare (♀ 431) in a mating with the old yellow lop male.

Female 175 was not actually mated with a black rabbit, but, had she been capable of producing black offspring, she should have done so in the matings with ♂ 177, a rabbit that did produce black young. Male 176 was mated with two does known to be capable of producing black offspring, with the result shown in table 34.

TABLE 34. — *Matings and young of ♂ 176, gray.*

Mating.	Gray.	Yellow.	Black.
With old ♀ lop, sooty . . .	11	3	0
Expected . . . . .	1	1	0
With ♀ 178, gray . . . . .	8	2	0
Expected . . . . .	3	1	0

(6) A sixth variety of gray rabbit produces gray, black, yellow, and sooty yellow offspring, but none of the other colors. It is heterozygous both in E and in A. It differs from variety 5 only in being heterozygous instead of homozygous in A. It may readily be produced by crossing yellow with black, or gray with sooty yellow, the result of these two crosses being identical. The formula of this variety is  $B_2Br_2E(R)AC_2I_2U_2Y_2$ . This variety is represented in our gray rabbits (♂ 177 and ♀ 178), which were borne by the Belgian hare (♀ 431) in the same litter as the rabbits of variety 5 already described, viz, ♀ 175 and ♂ 176. Another rabbit of this variety was the gray ♂ 505.

TABLE 35. — *Matings and young of ♂ 177, gray.*

Mating.	Gray.	Black.	Yellow.	Sooty.
With ♀ 175, gray (variety 5) .	5	0	2	0
Expected . . . . .	3	0	1	0
With ♀ 178, gray (variety 6) .	1	2	0	0
Expected . . . . .	9	3	3	1

Why rabbits 177 and 178 should differ in breeding capacity from their brother and sister, 176 and 175, is readily explained. The father was heterozygous as regards factor A. To 175 and 176, he transmitted it; to 177 and 178, he did not. But all four received this factor from their mother, a homozygous gray rabbit (♀ 431). Hence 175 and 176 were double in A, but 177 and 178 were single as regards A. Evidence for the classification given of rabbits 177 and 178 is shown in tables 35 and 36.

(7) A seventh variety of gray rabbit should produce young of the varieties gray, yellow, and white, but none of other colors. It should differ from variety 5 in being heterozygous (single) in C. Its formula would be  $B_2Br_2E(R)A_2CI_2U_2Y_2$ . We are unable to cite an undoubted example of this variety, though it could probably be produced by crossing variety 3 with variety 5, as well as in several other ways.

(8) An eighth variety bears the same relation to variety 6 that 7 does to 5. It is of the formula  $B_2Br_2E(R)ACI_2U_2Y_2$ , and it produces young of the 5 visibly different classes — gray, black, yellow, sooty yellow, and white. This variety

is represented in rabbits ♂ 1160 and ♀ 1171, born in the same litter with ♀ 1161 and ♂ 1172 of variety 4 (p. 55). When mated with each other they produced 7 gray, 1 black, 2 yellow, 1 sooty, and 5 white young. Other rabbits of this variety were produced by the Belgian hare (♀ 431) in a mating with an albino rabbit (♂ 56). These gray rabbits (2 males and 3 females, 232 to 236), when mated *inter se* produced 17 gray, 5 black, 6 yellow, 2 sooty yellow and 6 white young, the expected Mendelian proportions being 27:9:9:3:16. When mated with albinos these same gray rabbits produced 9 gray, 6 black, 2 yellow, and 16 white young. The zygotic composition of the albino mates in this case is not fully known, so that the theoretical proportions of the pigmented young can not be stated. The albinos are as expected approximately half the total young, and all expected color varieties are represented except sooty yellow.

TABLE 36. — *Matings and young of ♀ 178, gray.*

Mating.	Gray.	Black.	Yellow.	Sooty.
With ♂176, gray (variety 5) .....	8	0	2	0
Expected .....	3	0	1	0
With ♂177, gray (variety 6) .....	1	2	0	0
With ♂505, gray (variety 6) <sup>1</sup> .....	5	3	1	....
Total for last two matings .....	6	5	1	(?)
Expected .....	9	3	3	1
With ♂179, yellow .....	1	3	3	0
With ♂319, yellow .....	8	3	4	6
Total for last two matings .....	9	6	7	6
Expected .....	1	1	1	1

<sup>1</sup> Plus 3 yellow or sooty, died young.

For simplicity the young of all 5 gray rabbits are grouped together in the foregoing account. In reality, however, one of the males was heterozygous in factor U, and at least 1 male and 1 female were heterozygous in factor I, as is shown by the facts (1) that several of the young produced in matings with white individuals bore spots of white, the whitest of all being belted with white ("Dutch marked"); and (2) that one of the gray offspring of the gray parents was of a pale blue-gray color.

(9) The gray rabbits just described, which produced a blue-gray young one, in reality belong to a ninth variety of gray rabbit, indistinguishable in appearance from the other eight, but producing a different assemblage of young, viz, dilute-colored as well as intensely colored young in each of the pigmented varieties, and also albinos. The whole assemblage of visibly different varieties is gray, black, yellow, sooty yellow, blue-gray, blue, pale yellow, pale sooty yellow, and white. Not all of these varieties were obtained directly from the pair of rabbits in question, doubtless because too small a number of young was produced, but in later generations all were obtained. Thus from the single blue-gray individual, when mated within the same family, were obtained blues, pale sooties, and pale yellows, as well as individuals of normal intensity. The zygotic formula of this ninth variety of gray rabbit is  $B_2Br_2E(R)ACI(D)Y_2U_2$ . Since it indicates a heterozygous condition in 4 character-units, we should expect a pair of individuals of this formula to produce 16 different gametic combinations. Eight of these are represented in the enumerated 8 classes of pigmented young, 8 others would occur among the albinos which would differ from the pigmented classes in the absence of C, but all of which would look alike, though breeding differently in crosses with pigmented animals.



(10) The gray rabbit which produced spotted offspring in crosses with albinos was undoubtedly heterozygous in regard to the factor U, for experience has shown (in agreement with Hurst, :05) that uniform pigmentation is in the main dominant over spotting. We might then recognize as a tenth variety one of the formula  $B_2Br_2E(R)ACI_2U(S)Y_2$ .

(11) Had the rabbit in question produced pale-pigmented as well as spotted young (and such we have since derived from this stock of rabbits), we should need to modify the formula as given by writing I(D) instead of  $I_2$ , *i. e.*, intense (dilute recessive). The formula of such a rabbit would be



This indicates a heterozygous condition as regards 5 character-units, and rabbits of this formula should be capable of producing 32 different gametic combinations, 16 of which would be visibly expressed in different pigmented varieties, while an equal number lacking the factor C would produce albinos visibly alike but gametically different.

If, then, we were to carry to its logical conclusion the enumeration of the conceivable different varieties of gray rabbit, all alike in appearance but all different in breeding capacity, *i. e.*, of different zygotic formula, we should need to mention 32 varieties: 8 of these would correspond with the first 8 which have already been enumerated and the existence of which has (except for variety 7) been demonstrated, namely:

- (1) Gray producing gray only.
- (2) Gray producing gray and black.
- (3) Gray producing gray and white.
- (4) Gray producing gray, black, and white.
- (5) Gray producing gray and yellow.
- (6) Gray producing gray, black, yellow, and sooty.
- (7) Gray producing gray, yellow, and white.
- (8) Gray producing gray, black, yellow, sooty, and white.

Eight other varieties would produce the same sorts of young as these 8, but would produce in addition dilute pigmented ones of the same color types, *i. e.*, blue-grays as well as grays, blues as well as blacks, pale yellows (cream) as well as yellows, and pale sooties as well as sooty yellows.

The 16 remaining varieties would produce the same sorts of young as the 16 varieties already described, but would produce spotted as well as uniformly pigmented (self) individuals.

TABLE 37.

Color.	Observed.	Expected.
Gray .....	24	27
Black .....	8	9
Yellow .....	16	9
Sooty .....	2	3
Blue-gray .....	8	9
Blue .....	2	3
Cream .....	3	3
Pale sooty .....	2	1

Not every one of these 32 varieties of gray rabbit has actually been demonstrated to exist in the course of our experiments; 10, however, which we have shown to exist, have already been mentioned, and several others are known. For example, by crosses of black with pale yellow (cream) or of blue with yellow, we have obtained grays which produced the same sorts of young as variety 6, and in addition blue-grays, blues, creams, and pale sooties. Such was the character of our gray females 1413, 1457, 1525, 1526, and 2009. By a male of like character they have produced young as shown in table 37.

Other gray rabbits produced by the same crosses, black  $\times$  cream, or blue  $\times$  yellow, produce the same assortment of young, and in addition albinos. That is, they are like variety 8, but heterozygous in intensity of pigmentation. These gray rabbits, females 1423, 1443, and 1505, and males 1351 and 1458, mated *inter se*, have produced young as indicated in table 38.

TABLE 38.

Color.	Observed.	Expected.
Gray .....	20	27
Black .....	8	9
Yellow .....	12	9
Sooty .....	1	3
Blue-gray .....	7	9
Blue .....	4	3
Cream .....	(?)	3
Pale sooty .....	1	1
White .....	8	21

The category yellow is probably too large because of a failure on our part to discriminate between yellow and cream, a difference which at first we failed to record. It is possible also that albino young were not enumerated in all the records which we have combined, and so albinos are apparently deficient in number.

It is needless to go farther in the enumeration of zygotic varieties of gray rabbits. There is little doubt that the entire 32 varieties theoretically possible could readily be produced; or we have found that a spotted coat may be transferred from one color variety to another by means of crosses, and the same is true of a dilute condition of the pigmentation in contrast to intense pigmentation. It is known also from a variety of sources, including besides our own observations the valuable experiments of Hurst (:05), that albinism may occur as a recessive character in any and all color varieties of rabbits. Additional evidence seems to be desirable chiefly as concerns the assumed factor E; therefore, we may proceed to the consideration of color varieties other than gray, in the course of which this evidence will be produced.

## BLUE-GRAY.

A blue-gray rabbit differs from a gray one only in the intensity of its pigmentation, which is always dilute. As regards the intensity factor, therefore, it is invariably homozygous,  $D_2$ , since  $D$  is recessive to  $I$ , whereas a gray rabbit may be either homozygous,  $I_2$ , or heterozygous,  $I$  ( $D$ ). Consequently only half as many zygotic combinations are possible among blue-gray as among gray rabbits, 16 instead of 32 being the maximum.

The 16 conceivable varieties of blue-gray rabbits, all of which should be similar in appearance but different in breeding capacity, are:

- (1) Blue-gray producing only blue-gray; formula,  $B_2Br_2E_2A_2C_2D_2U_2Y_2$ .
- (2) Blue-gray producing blue-gray, and blue; formula,  $B_2Br_2E_2AC_2D_2U_2Y_2$ .
- (3) Blue-gray producing blue-gray, and white; formula,  $B_2Br_2E_2A_2CD_2U_2Y_2$ .
- (4) Blue-gray producing blue-gray, blue, and white; formula,  $B_2Br_2E_2ACD_2U_2Y_2$ .
- (5) Blue-gray producing blue-gray, and cream; formula,  $B_2Br_2E(R)A_2C_2D_2U_2Y_2$ .
- (6) Blue-gray producing blue-gray, blue, cream, and pale sooty; formula,  $B_2Br_2E(R)AC_2D_2U_2Y_2$ .
- (7) Blue-gray producing blue-gray, cream, and white; formula,  $B_2Br_2E(R)A_2CD_2U_2Y_2$ .
- (8) Blue-gray producing blue-gray, blue, cream, pale sooty, and white; formula,  $B_2Br_2E(R)ACD_2U_2Y_2$ .

The 8 remaining varieties would be identical with these, except for the factor  $U$ , in which they would be heterozygous,  $U$  ( $S$ ), producing spotted as well as self-pigmented young.

Three blue-gray rabbits, all females, have been tested, and each of these is of a different zygotic formula.

Female 389, the original blue-gray individual, proved to be of variety 4. When mated with ♂ 248, a black animal heterozygous in  $E$ ,  $C$ , and  $I$ , *i. e.*, of formula  $B_2Br_2E(R)CI(D)U_2Y_2$ , she produced gray, blue-gray, blue, and white young, all the expected classes except black being produced. The observed numbers of the young and the expected proportions are given in table 39.

TABLE 39.

Color.	Observed.	Expected.
Gray .....	4	27
Blue-gray .....	1	9
Black .....	0	9
Blue .....	4	3
White .....	1	16

Female 656 was of variety 2, heterozygous in  $A$  only, as is shown by table 40.

Of the 4 males with which ♀ 656 was mated, all but ♂ 1340 produced albino young in other matings. This indicates clearly that ♀ 656 was

not heterozygous in C. The matings with males 402, 1340, and 248 show that she was homozygous in E.

TABLE 40. — *Matings and young of blue-gray ♀ 656.*

Mating.	Gray.	Blue-gray.	Black.	Blue.
With sooty ♂4020.....	5	0	2	4
With sooty ♂134.....	1	0	1	0
With black ♂248.....	4	0	0	3
With blue ♂1228.....	0	3	0	3

Female 1437 was either of variety 6 or else of variety 8, *i. e.*, she was known to be heterozygous in E and in A, but was insufficiently tested as regards C. Mated with blue ♂ 1434 she produced 2 blue-gray and 1 pale sooty young and 1 pigmented animal of uncertain character.

#### BLACK.

Black rabbits, as we have already observed, differ from gray ones only in the factor A, which they lack completely. 16 different zygotic combinations are theoretically possible among them.

- (1) Black producing nothing but black; formula,  $B_2Br_2E_2C_2I_2U_2Y_2$  (compare diagram, p. 52).
- (2) Black producing black, and white; formula,  $B_2Br_2E_2CI_2U_2Y_2$ .
- (3) Black producing black, and sooty; formula,  $B_2Br_2E(R)C_2I_2U_2Y_2$ .
- (4) Black producing black, sooty, and white; formula,  $B_2Br_2E(R)CI_2U_2Y_2$ .
- (5) Black producing black, and blue; formula,  $B_2Br_2E_2C_2I(D)U_2Y_2$ .
- (6) Black producing black, blue, and white; formula,  $B_2Br_2E_2CI(D)U_2Y_2$ .
- (7) Black producing black, blue, sooty, and pale sooty; formula,  
 $B_2Br_2E(R)C_2I(D)U_2Y_2$ .
- (8) Black producing black, blue, sooty, pale sooty, and white; formula,  
 $B_2Br_2E(R)CI(D)U_2Y_2$ .

The 8 remaining varieties would be identical with these 8, except that they would be heterozygous as regards U, viz, U(S) instead of U. Consequently they would produce spotted as well as self-pigmented young.

All the black rabbits (with one exception) which we have used for breeding purposes were produced in the course of our experiments from animals of other color varieties. All were in one or more respects heterozygous, except possibly the recently purchased black rabbit, not yet fully tested, but apparently homozygous in all particulars and so of variety 1. Hurst (:05) obtained rabbits of variety 2, but we do not happen to have had any of this variety, nor of variety 3.

Variety 4 is represented in a modified form in our rabbits 104, 105, 167, 247, and 255. The modification consists in this: the albino offspring are, at least in part, of the Himalayan type, having pigmented extremities.

This we might express by adding the Himalayan factor ( $C'$ ) to the formula as given for variety 4. Variety 5 is represented in our black X, which when mated with blue ♂ 1434 (variety 3) produced 4 black and 4 blue young.

Variety 7 is represented in our rabbits 1230 and 1231, 2011, and 2038; and variety 8, in a modified form, in our ♂ 248, which has sired black, blue, sooty, pale sooty, white, and Himalayan white offspring by black, sooty-yellow, or blue-gray mates. He therefore differs from variety 8 as previously described in that he is heterozygous in the Himalayan factor  $C'$ . His formula accordingly is  $B_2Br_2E(R)C'(C)I(D)U_2Y_2$ . Some evidence for this classification of our black animals will be found in the table 41. Other evidence is derived from matings with yellow or gray animals.

TABLE 41. — *Matings of black rabbits with black or sooty individuals.*

Mating.	Black.	Sooty.	Himalayan.	White.	Blue.	Pale sooty.
♀ 105 black with ♂ 104 black .....	9	1	1	....	....	....
♀ 167 black with ♂ 248 black .....	2	3	....	2	....	....
♀ 247 black with ♂ 248 black .....	3	2	1	....	....	....
♀ 255 black with ♂ 248 black .....	10	1	2	....	....	....
Total .....	24	7	4	2	....	....
Expected proportions.....	9	3	3	1	....	....
♀ 1230 black with ♂ 1340 sooty.....	3	4	....	....	....	....
Expected .....	1	1	....	....	....	....
♀ 1230 black with ♂ 1414 sooty.....	4	4	....	....	1	....
Expected .....	3	3	....	....	1	1

#### BLUE.

“Blue” pigmentation in rabbits and other rodents is merely a dilute condition of black. The zygotic formula of a blue rabbit is the same as that of a black one, if we substitute  $D_2$  for the  $I_2$  or  $I(D)$  of the black varieties. Blue rabbits may occur theoretically of 8 different sorts, viz:

- (1) Blue producing blue only; formula,  $B_2Br_2E_2C_2D_2U_2Y_2$ .
- (2) Blue producing blue, and white; formula,  $B_2Br_2E_2CD_2U_2Y_2$ .
- (3) Blue producing blue, and pale sooty; formula,  $B_2Br_2E(R)C_2D_2U_2Y_2$ .
- (4) Blue producing blue, pale sooty, and white; formula,  $B_2Br_2E(R)CD_2U_2Y_2$ .

TABLE 42. — *Matings and young of ♂ 1434, blue.*

Mating.	Black.	Blue.	Sooty.	Pale sooty.
With ♀ 647, sooty, variety 2.....	3	....	3	....
Expected.....	1	....	1	....
With ♀ 1471, sooty, variety 3 or 4.	4	2	5	2
Expected.....	1	1	1	1
With ♀ black, variety 5 or 6.....	4	3	....	....
Expected.....	1	1	....	....



The 4 remaining varieties would be identical with these 4 except as regards the factor U, in which they would be heterozygous, U(S), instead of homozygous, U<sub>2</sub>.

We have determined the zygotic formulæ of 2 blue rabbits only, both of which were produced in the course of our experiments. One (♂ 1434, table 42) was of variety 3, the other (♂ 1228, table 43) was of variety 4.

We shall pass by the spotted black and spotted blue varieties of rabbit, of both which sorts a certain number of individuals have been produced in our experiments, but which have not been thoroughly tested.

TABLE 43. — *Matings and young of ♂ 1228, blue.*

Mating.	Blue-gray.	Black.	Blue.	Sooty.	Pale sooty.	White.
With ♀ 647, sooty, variety 2.....	....	15	....	17	....	3
Expected .....	....	3	....	3	....	2
With ♀ 1280, sooty, variety 3 or 4 .....	....	2	2	2	0	....
Expected .....	....	1	1	1	1	....
With ♀ 656, blue-gray, variety 2 .....	3	....	3	....	....	....
Expected .....	1	....	1	....	....	....

#### YELLOW.

Yellow rabbits differ from gray ones only in the factor E (extended black or brown pigmentation), in place of which they bear the alternative condition R (restricted black or brown pigmentation). Since R is recessive in relation to E, yellow rabbits are invariably homozygous, R<sub>2</sub>, as regards this factor. Theoretically sixteen different varieties are possible, as follows:

- (1) Yellow producing yellow only; formula, B<sub>2</sub>Br<sub>2</sub>R<sub>2</sub>A<sub>2</sub>C<sub>2</sub>I<sub>2</sub>U<sub>2</sub>Y<sub>2</sub>.
- (2) Yellow producing yellow, and white; formula, B<sub>2</sub>Br<sub>2</sub>R<sub>2</sub>A<sub>2</sub>CI<sub>2</sub>U<sub>2</sub>Y<sub>2</sub>.
- (3) Yellow producing yellow, and sooty; formula, B<sub>2</sub>Br<sub>2</sub>R<sub>2</sub>AC<sub>2</sub>I<sub>2</sub>U<sub>2</sub>Y<sub>2</sub>.
- (4) Yellow producing yellow, sooty, and white; formula, B<sub>2</sub>Br<sub>2</sub>R<sub>2</sub>ACI<sub>2</sub>U<sub>2</sub>Y<sub>2</sub>.

Four other varieties should differ from these 4 in factor I only, being I(D) instead of I<sub>2</sub>, and producing dilute as well as intensely pigmented individuals. Eight others should differ from these eight in producing spotted as well as uniformly pigmented individuals. We shall content ourselves with giving examples of the first four varieties enumerated.

Variety 1 produces only yellows when mated with other yellows or with sooties, and only yellows and grays when mated with blacks or blues of any sort whatever. It is represented in our yellow ♂ 381, a son of 2 gray rabbits of variety 5, viz, ♀ 175, and ♂ 176. He was mated with 6 different yellow females, 3 of which had produced sooty offspring by other mates, and there resulted 61 young, all yellow. In matings with 2 different sooty females he produced 12 young, all yellow; and in a mating with a gray female of variety 6 (♀ 178) he produced 3 yellow and 6 gray

young; expected 1:1. We have had several other yellow rabbits which were probably of this same variety, but they were less extensively and inconclusively tested.

Variety 2 is represented in a yellow rabbit obtained by purchase ( $\sigma$  1256). He was mated with  $\varphi$  547 yellow, variety 3, and produced 9 young, all yellow (as expected); by yellow  $\varphi$  745 $\frac{1}{2}$ , variety 4, he produced 4 yellow and 3 white young (expected 3:1); and by black  $\varphi$  1230 and  $\varphi$  1231, variety 7, he produced 8 yellow, 3 gray, and 1 blue-gray young; expected 4:3:1.

Variety 3 is represented in yellow females 547, 714, and 1115, which in matings with yellow males of variety 4 produced 24 yellow and 2 sooty young, but no white ones. Had these females been of variety 4 they should have produced 25 per cent of white young in the mating mentioned. It is possible that the recorded number of sooties is too small, owing to a failure in our earlier records to discriminate sooty from yellow. No such possibility exists in the case of the records for albinos. One of the females already mentioned, of variety 3 ( $\varphi$  1115), when mated with sooty  $\sigma$  1340 produced 2 yellow and 6 sooty young.

Another yellow rabbit of variety 3 was the lop  $\sigma$  179 (plate 2, fig. 8). When mated with the sooty "old female lop" (plate 1, fig. 2) he produced 4 yellow and 4 sooty young (expected 1:1); and when mated with black females of variety 4 ( $\varphi$  105, 167, and 247) he produced 7 gray, 5 black, 6 yellow, and 7 sooty young (expected 1:1:1:1). Notice in the matings with black females the total absence of albinos, though all these females had produced albinos by other mates.

Still another male of variety 3,  $\sigma$  319, son of the sooty old female lop by gray  $\sigma$  176, variety 5, when mated with the black  $\varphi$  247 (variety 4) produced 2 gray, 2 black, 2 yellow, and 1 sooty young (expected 1:1:1:1).

Variety 4 is represented in our "Cutler's yellow" and in  $\varphi$  745 $\frac{1}{2}$  produced by black  $\varphi$  105 (variety 4) mated with yellow  $\sigma$  319 (variety 3). When "Cutler's yellow" was mated with the above female, 745 $\frac{1}{2}$ , he produced 4 yellow, 3 sooty, and 1 white young (expected 9:3:4). When mated with sooty females 632 and 647 (variety 2), he produced 7 yellow, 7 sooty, and 2 white young (expected 3:3:2).

#### SOOTY.

Sooty rabbits differ from yellow ones only in the factor A, which they lack. Theoretically 8 varieties are possible, viz:

- (1) Sooties producing sooties only, when mated *inter se*; formula,  $B_2Br_2R_2C_2I_2U_2Y_2$ .
- (2) Sooties producing sooty, and white; formula,  $B_2Br_2R_2CI_2U_2Y_2$ .
- (3) Sooties producing sooty, and pale sooty; formula,  $B_2Br_2R_2C_2I(D)U_2Y_2$ .
- (4) Sooties producing sooty, pale sooty, and white; formula,  $B_2Br_2R_2CI(D)U_2Y_2$ .

The 4 remaining varieties would be like these, except as regards the factor U, in which they would be heterozygous, U(S), instead of homozy-



gous,  $U_2$ . They would produce spotted as well as uniformly pigmented young.

An example of variety 1 is the "old female lop" (plate 1, fig. 2). When mated with an albino of black ancestry, ♂ 45 (plate 1, fig. 3), she produced a litter of 8 black young (plate 1, fig. 1). This experiment shows her to have been homozygous in C, *i. e.*, to have been  $C_2$  in character, and to have lacked factor A. When mated with yellow ♂ 179 (plate 2, fig. 8), variety 3, she produced 4 yellow and 4 sooty young, exactly the expected equality of yellow and sooty. Another individual probably of this same variety was ♀ 1472, which when mated with a sooty male, 1414, produced 12 young, all sooty. The male just mentioned belonged apparently to variety 3, for when mated with the black ♀ 1230 (variety 7) he produced 5 black, 6 sooty, and 1 blue young (expected 3:4:1; or if pale sooties were differentiated from sooties, which we probably failed to do in making the records, 3 black:3 sooty:1 blue:1 pale sooty).

Variety 2 is represented in our ♂ 402 and ♀ 632 and 647. When ♂ 402 was mated with ♀ 632, they produced a litter of 4 sooty and 1 white young (expected 3:1). Female 647, when mated with "Cutler's yellow" (variety 4), produced 5 yellow, 4 sooty, and 1 white young (expected 3:3:2). The white individual produced by ♀ 632 and ♂ 402 was a Himalayan albino. This shows one or both of the parents to have been slightly different from typical variety 2, and to have carried  $C'$ .

Variety 3 is represented probably by our ♀ 1471 which, when mated with blue ♂ 1434, produced 4 black, 2 blue, 5 sooty, and 2 pale sooty young (expected 1:1:1:1). The possibility is not excluded that this female was of variety 4 (capable of producing also albino young), but she can not have been of either variety 1 or variety 2. Another probable example of variety 3 is ♀ 1280. (See matings of ♂ 1228, blue, p. 63).

Variety 4 we have not identified with certainty. Neither have we made a detailed study of pale yellows, pale sooties, or spotted rabbits of any color variety. We have observed, however, that dilute pigmentation, as well as spotting, occurs in all the fundamental color varieties and are entirely satisfied of the independent inheritance of both.

#### WHITE.

Albino rabbits differ from pigmented ones only in regard to the factor C, which they either lack, or possess only in a greatly modified form,  $C'$ . If C is absent, there are possible 16 different combinations of the 4 remaining variable factors, which combinations correspond with gametes of the 16 visibly different pigmented varieties of rabbit, minus C. But if C is present in the modified form,  $C'$ , found in Himalayan albinos, 16 other gametic combinations should be possible, only slightly different from the foregoing, making in all 32 different gametic possibilities, or 232 zygotic possibilities.

Plainly it is unprofitable to attempt to find illustrations of all these conceivable variations. We shall content ourselves with noticing some of the more important varieties of albinos and presenting evidence that each of the 4 variable factors, A, E, I, and U, is transmitted through albinos.

The following albino varieties may be expected to occur:

- (1) White producing gray only (in crosses with any pigmented variety); formula,  $B_2Br_2E_2A_2I_2U_2Y_2$ .
- (2) White producing black only (in crosses with black or any pigmented variety recessive to black); formula,  $B_2Br_2E_2I_2U_2Y_2$ .
- (3) White producing yellow only (in crosses with yellow or sooty individuals); formula,  $B_2Br_2R_2A_2I_2U_2Y_2$ .
- (4) White producing sooty only (in crosses with sooty); formula,  $B_2Br_2R_2I_2U_2Y_2$ .
- (5) White producing gray, and black (in crosses with black or any pigmented variety recessive to black); formula,  $B_2Br_2E_2AI_2U_2Y_2$ .
- (6) White producing gray, and yellow (in crosses with yellow or sooty); formula,  $B_2Br_2E(R)A_2I_2U_2Y_2$ .
- (7) White producing gray, black, yellow, and sooty (in crosses with sooty); formula,  $B_2Br_2E(R)AI_2U_2Y_2$ .
- (8) White producing black, and sooty (in crosses with sooty); formula,  $B_2Br_2E(R)I_2U_2Y_2$ .
- (9) White producing yellow, and sooty (in crosses with sooty); formula,  $B_2Br_2R_2AI_2U_2Y_2$ .

Another set of 9 varieties, quite similar to these, would produce only pale-pigmented offspring. As regards the intensity factor they would be  $D_2$  instead of  $I_2$ . Another set of 9 varieties would produce both dilute and intensely pigmented offspring, being heterozygous,  $I(D)$ , as regards the intensity factor.

Nine other varieties, in which  $S_2$  replaces  $U_2$ , would produce only spotted young; and another set of 9 would produce both spotted and self-colored offspring; in these  $U(S)$  would replace  $U_2$ . Another set of 9 varieties would produce only pale-pigmented spotted individuals, another would produce pale-pigmented individuals, both self and spotted; and lastly a set of 9 varieties would produce both dilute and strongly pigmented individuals, both spotted and self-colored.

It is probable that the foregoing list of 72 varieties could be duplicated in varieties having the Himalayan modification, and duplicated a second time in varieties heterozygous in the two sorts of albinism.

A few examples will now be mentioned of some of the 9 varieties of albinos first enumerated, or of animals differing from those 9 varieties in one or two characters only.

Variety 1 is represented in our ♂ 1425, which when mated with black ♀ 1541 produced 11 young, all gray, and when mated with yellow ♀ 547 (variety 3) produced 4 young, all gray. Variety 2, but heterozygous in the Himalayan modification,  $C'$ , and in spotting with white,  $U(S)$ , is rep-

resented in our ♂ 45 (plate 1, fig. 3), which when mated with the sooty lop (plate 1, fig. 2) produced 8 young, all black. One of these is shown in plate 1, fig. 1. When mated with black ♀ 105, he produced 8 black pigmented and 3 Himalayan albino young, but several of the pigmented young were spotted with white, this character being recessive in ♀ 105, which had a Dutch-marked father.

Variety 5 is represented in ♀ 269, which when mated with sooty ♂ 402 produced 1 gray and 3 black young (expected 1:1). When mated with yellow ♂ 179 (variety 3) she produced in one litter 3 black young, and in a second litter, 3 gray and 1 black. This second litter, in which the expected proportions of gray and of black young are exactly realized, is shown in plate 2, fig. 6, the parents being shown in figs. 5 and 8 of the same plate.

Variety 8 is probably represented in ♀ 268 which when mated with yellow ♂ 319 (variety 3) produced 2 gray, 1 yellow, 2 black, and 2 sooty young (expected 1:1:1:1). The only other possibility is that this female was of variety 7, which should in this mating produce the same varieties of young, but in the proportions, 9:3:3:1.

Variety 8 (but heterozygous in C', the Himalayan factor) is represented in ♀ 108, which when mated with black ♂ 104 (variety 4) produced 3 black, 3 sooty, and 6 Himalayan albino young, exactly the expected proportions. By yellow ♂ 179 (variety 3) she produced 1 gray, 1 yellow, and 1 sooty young (expected 1:1:1:1 black).

The foregoing cases would afford confirmation (if confirmation were necessary) of the discovery by Cuénot (:03) and by Hurst (:05) that albino mammals transmit color factors, and that they vary in zygotic composition as regards color factors. That albinos transmit the factor A is shown by the observation that some of them (which bear A) produce gray offspring in crosses with black pigmented animals, while others (lacking A) never produce gray offspring, though mated to the same black animals.

That albinos transmit the factor E is shown clearly by extensive experiments with guinea-pigs carried out by one of us. One family of albino guinea-pigs has been found invariably to produce black offspring in matings with any pigmented variety devoid of factor A, whether that variety has the extended or the restricted distribution of black or brown pigment; a second family of guinea-pigs, with equal uniformity, produces colored offspring having a restricted distribution of black pigment, if crossed with colored individuals having the restricted distribution. This second variety produces black-eyed yellows, if crossed either with black-eyed yellow or with brown-eyed yellow individuals. Of the 2 albino varieties mentioned, the first evidently carries B with E, the second B with R.

These same two families of albino guinea-pigs likewise differ in factor I, which is present in the first family, but replaced by D in the second. If each is crossed with pale yellow (cream) individuals, the former produces

in  $F_1$  black offspring, and in  $F_2$  black, blue, red, and cream, as well as albinos; whereas the latter produces in  $F_1$  cream, and in  $F_2$  cream and albino offspring only.

As regards the factor U, Hurst (:05) has shown clearly that some albino rabbits transmit a uniformly colored coat, others a spotted coat, in crosses with colored rabbits. The former we may regard as carrying U, the latter S. In rabbits we have not made an extensive study of this matter. We have found, however, in agreement with Hurst, and Woods (:03) that spotted rabbits in general produce only spotted young, when mated with each other, *i. e.*, that spotting with white is recessive to uniform pigmentation, and the case has been mentioned of an albino ( $\sigma$  45) which produced spotted young when mated with a black rabbit that had a spotted father.

In guinea-pigs also, spotting is in the main recessive, and spotting is clearly transmitted by albinos. Thus the  $\sigma$  2002, figured and described by Castle (:05), produced spotted young when mated with spotted females, and among his grandchildren spotted animals were very common, no matter whether the female grandparent and the parents were spotted or not.

All the varied evidence which has been obtained from the study of rabbits, guinea-pigs, rats, and mice, by others as well as by ourselves, supports the hypothesis that albinos differ from pigmented individuals, by a single factor only, which factor we call C.

#### THE MATERIAL BASIS OF HEREDITY FACTORS.

In what form, it may be asked, are we to suppose that the various assumed factors exist. Do they occur as so many different substances lying side by side but unmixed in every reproductive cell? To this question we may give at present no satisfactory answer.

It is, however, we think, not necessary to suppose that there exist in the minute germ-cell as many complex organic substances as there are activities of the cell; neither is it necessary to suppose a different substance present for every independent factor identified. The various independent factors may have a basis no more complicated than that of so many atoms attached to a complex molecular structure. Experiment shows that the factors may be detached one by one from the organic complex. The discontinuity of their coming and going is entirely in harmony with the conception of them as components merely of complex molecular bodies.



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## DESCRIPTION OF PLATES.

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### PLATE 1. — *Photographs from life of rabbits described in the text.*

- FIG. 1. ♂ 248, son of the rabbits shown in figs. 2 and 3; ears of intermediate length, hair short, color black.
2. "Old female lop," sooty yellow in color.
  3. ♂ 45, a short-eared, Himalayan albino, angora rabbit.
  4. ♀ 400, daughter of ♂ 248, fig. 1, and of his sister ♀ 247, a rabbit of like character.

### PLATE 2. — *Photographs from life of rabbits described in the text.*

- FIG. 5. ♀ 269, a short-eared albino rabbit.
6. A litter of four rabbits (640 to 643) borne by ♀ 269, fig. 5, when mated with ♂ 179, fig. 8. Three are gray, one is black; all have ears of intermediate length, as compared with the parents.
  7. Gray quarter-blood lops borne by ♀ 431, plate 3, fig. 9, in a mating with her son ♂ 176, a half-blood lop similar in appearance to his sister ♀ 175, plate 3, fig. 10.
  8. ♂ 179, a full-blood yellow lop, son of the "old female lop," plate 1, fig. 2, and of the "old male lop," a yellow rabbit.

### PLATE 3. — *Photographs from life (except fig. 9) of rabbits described in the text.*

- FIG. 9. Mounted skin of ♀ 431, the "Belgian hare," a gray rabbit with short ears.
10. ♀ 175, a gray half-blood lop, daughter of ♀ 431, fig. 9, and the old ♂ lop, a yellow rabbit similar in appearance to his son ♂ 179, plate 2, fig. 8.
  11. ♀ 322, a gray three-quarter blood lop, daughter of old female lop, plate 1, fig. 2, and the half-blood lop ♂ 176; compare fig. 10, which gives a good idea of the appearance of ♂ 176.
  12. ♂ 381, son of ♀ 175, fig. 10, and her brother, ♂ 176; an F<sub>2</sub> half-blood lop, with the same general ear-character as his parents, but yellow in color, like his grandfather.

### PLATE 4. — *Dorsal and ventral views of the skulls of 3 rabbits.*

In the middle the skull of ♂ 248 (compare plate 1, fig. 1); at the right the skull of his mother "old female lop" (plate 1, fig. 2); and at the left the skull of his father ♂ 45 (plate 1, fig. 3).













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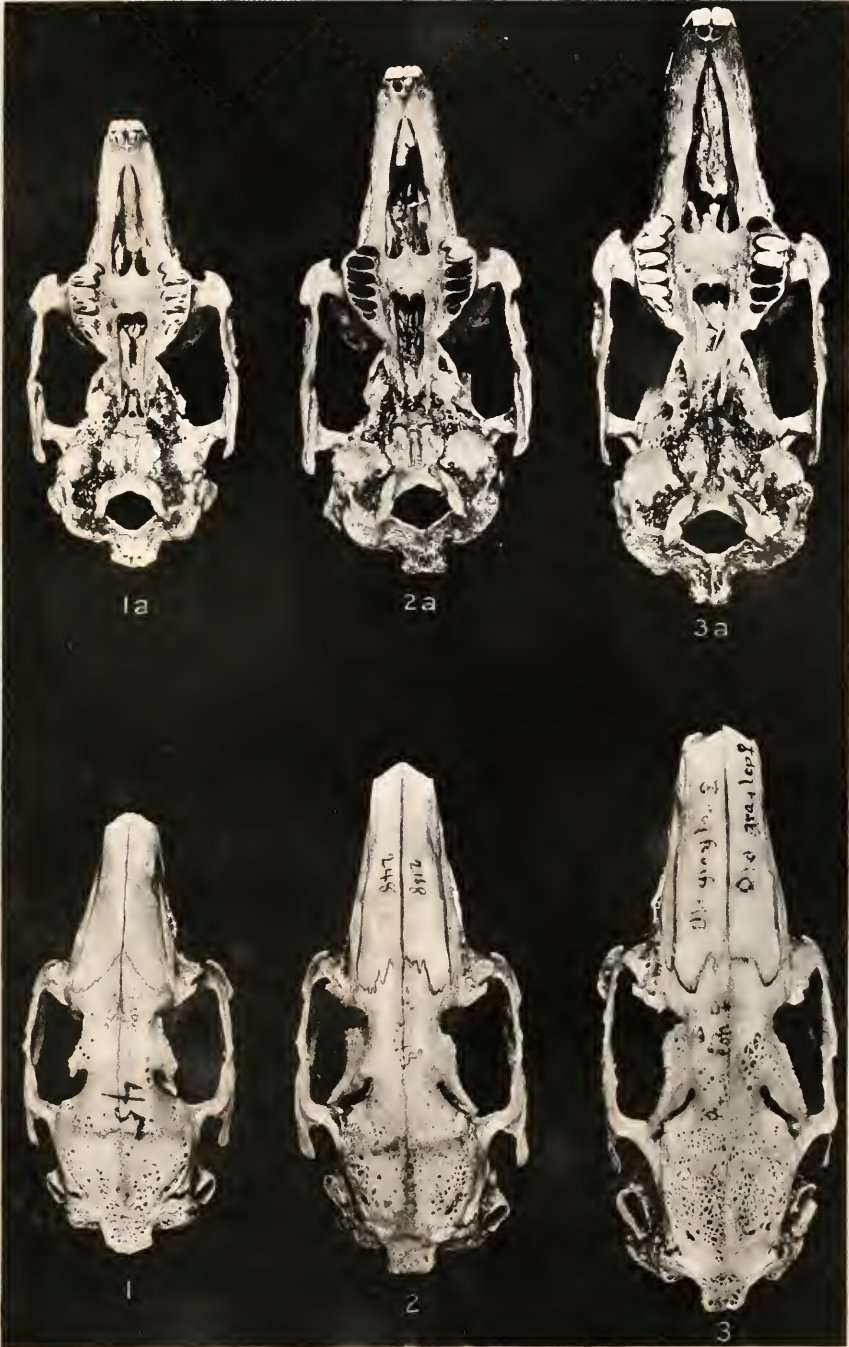
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